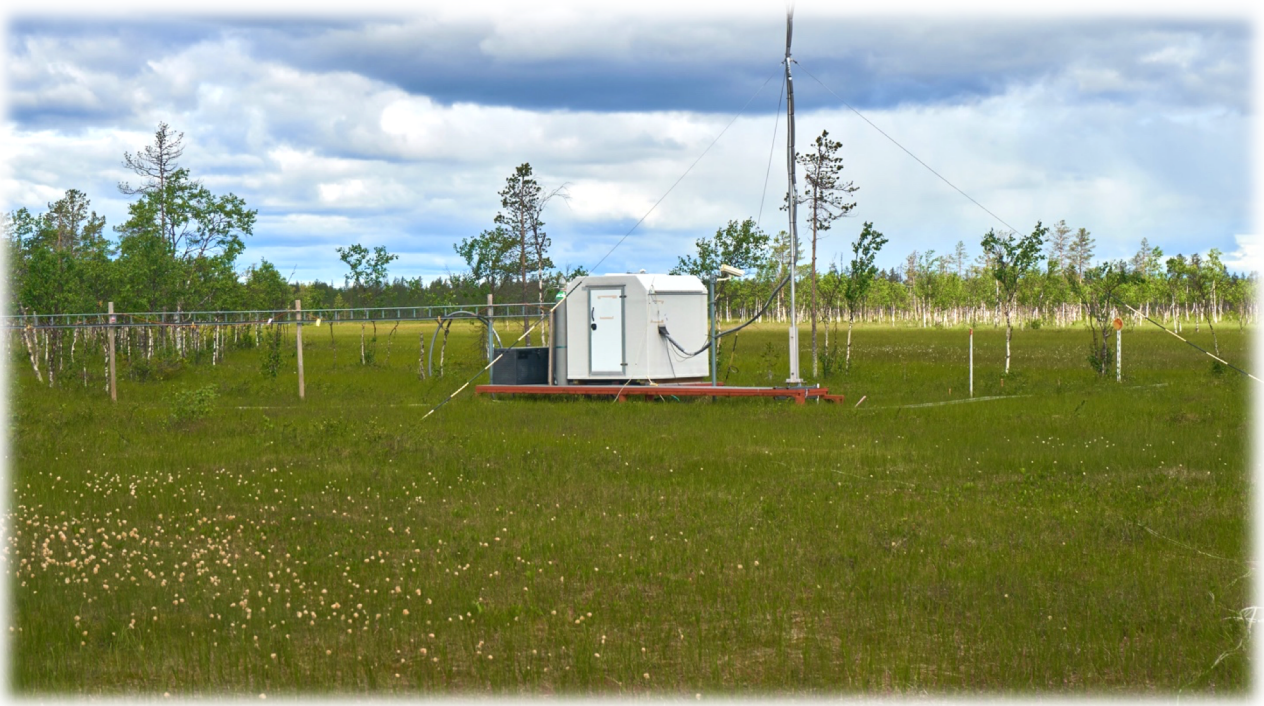
Importance of vegetation properties and redox potential to CH_4 flux at a boreal fen

Hanna Finne



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Tiivistelmä – Referat – Abstract

Boreal mires are natural sources of methane and contribute considerably to the global methane budget. Therefore, in order to comprehend the overall impact that these ecosystems have on climate change, it is essential to understand the factors that influence processes involved in methane production and consumption. Factors affecting methane flux vary between different mires, but there is also great spatial and temporal variation in flux within mires. In previous studies, temperature and water table position have been shown to influence methane flux, but vegetation could aid in explaining the small-scale variation. Vegetation can indicate spatial variation in water table position, but also affect methane flux directly by the transportation of methane through plant tissues, and by providing substrate for microorganisms through primary production. Furthermore, redox potential is a poorly studied factor that can reflect if chemical conditions in peat are suitable for methane production or consumption, making it a useful tool in predicting methane flux. In this thesis, I seek to identify if small-scale spatial variation in the methane flux occurs within the studied mire area. In addition, I strive to identify important controllers of the observed spatiotemporal variation in methane flux, with a specific focus on the effect of vegetation properties and redox potential.

Methane and carbon dioxide fluxes were measured with the closed chamber technique at a boreal fen in Sodankylä (67°22'06.6"N 26°39'16.0"E) during the growing season in 2019. Flux measurements were carried out at nine measurement plots belonging to three different vegetation types: flark, lawn and string. Coverage and height of plant functional groups were followed during the summer and continuous redox potential was measured for each plot. CH_4 fluxes of different plots and vegetation types were compared to study the spatial variation in methane flux. Generalized additive models (GAM) were used to determine which variables are best to explain spatiotemporal variation in methane flux over the growing season.

Mean methane flux during the summer was 0.94 ± 0.01 μg CH_4 m^{-2} s^{-1} which is in the same magnitude as observed in a previous study at the fen. Some small-scale spatial variation in the methane fluxes was observed at the study site, with strings having lower flux than flaks and lawns. However, overall the spatial variation was small, while temporal variation in methane flux over the growing season was considerable. The best model, that was a combination of vegetation, redox potential and environmental variables, and it explained 72 % of the observed variation in methane flux. Vascular plant variables were the most important variables in the model, whereas moss functional groups were of lesser importance. Redox potential in deeper peat layers was also important in the model, but redox potential closer to the surface was not found to be significant.

Vegetation is an important controller of methane flux, and this information could potentially be used when predicting methane flux over larger areas by using remote sensing to map vegetation characteristics. Redox potential, on the other hand, is relatively easy to measure, and the result suggests that it could provide a useful tool for improving the predictions of methane flux.

Avainsanat – Nyckelord – Keywords
Methane, boreal mires, vegetation, redox potential, climate change

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Tiivistelmä – Referat – Abstract

Metan bildas naturlig vid boreala myrmarker och dessa ekosystem bidrar avsevärt till den globala metanbudgeten. För att uppskatta boreala myrmarkers inverkan på klimatförändring är det viktigt att förstå vilka faktorer som kan påverkar de processer som bidrar till metanproduktion och -konsumtion. Faktorer som påverkar metanflöde varierar mellan olika myrmarker, men de kan också förekomma stor spatial och temporal variation i metanflöde inom en och samma myrmark. Temperatur och vattennivå har i tidigare studier visats påverka metanflödet, men vegetationens egenskaper skulle kunna förklara småskalig variation i metanflöde. Vegetation kan nämligen reflektera spatial variation i vattennivå, och kan dessutom påverka metanflödet direkt genom att transportera metan till atmosfären via växtvävnader och med att genom primärproduktion producera substrat för mikroorganismer. Därtill är redoxpotential en dåligt studerad faktor som kan beskriver de kemiska förhållandena i torv och därmed reflektera om förhållandena är tillfördelaktiga för metanproduktion eller -konsumtion. Därmed kan redoxpotential möjligen vara en användbar indikator av metanflöde. I denna avhandling utforskar jag om småskalig spatial variation i metanflödet förekommer inom den studerade myrmarken. Dessutom strävar jag efter att identifiera faktorer som kan användas för att förklara spatiotemporal variation i metanflödet under tillväxtperioden, med fokus på betydelse av vegetationens egenskaper och redoxpotential.

Under tillväxtperioden av 2019 mättes metan- och koldioxidflöde med den slutna kammartekniken vid en boreal myrmark i Sodankylä (67°22'06.6"N 26°39'16.0"E). Flödesmätningar genomfördes vid nio mätningsplatser som tillhörde tre olika vegetationstyper: flarkar, mellanytor och strängar. Täckning och höjd av växternas funktionella grupper följdes under sommaren och redoxpotential mättes kontinuerligt vid varje mätningsplats. Metanflöde mellan mätningsplatser och vegetationstyper jämfördes för att studera spatial variation och GAM (generalized additive models) modeller användes för att bestämma vilka variabler som kan förklara spatiotemporal variation i metanflödet.

Under tillväxtperioden var metanflödet i medeltal 0.94 $\pm$ 0.01 μg CH_4 m^{-2} $s^{-1,}$ vilket är i samma storlek som observerats i en tidigare studie vid myrmarken. Metanflöde från strängar var i medeltal lägre än för flarkar och mellanytor, och därmed förekom småskalig spatial variation i metanflödet vid studieplatsen. Överlag var den spatiala variationen trots allt liten, medan temporal variation i metanflöde under tillväxtperioden var betydlig. Den bästa modellen var en kombination av vegetations-, redoxpotential- och miljövariabler och den förklarade 72% av den observerade variationen i metanflödet. De viktigaste variablerna i modellen var kärlväxternas funktionella grupper. Däremot var mossornas betydelse i modellen mindre. Dessutom var redoxpotential i djupare torvlager också viktig, medan redoxpotential närmare ytan inte visade sig vara signifikant.

Vegetationens egenskaper kan avsevärt påverka metanflödet, och denna information kan användas för att förutspå metanflöde över större områden genom att kartlägga vegetationens egenskaper med hjälp av fjärranalyser. Redoxpotentialen är, i sin tur, relativt lätt att mäta, och resultaten tyder på att det kan vara ett användbart verktyg för att förbättra uppskattningar av metanflöde.

Avainsanat – Nyckelord – Keywords
Metan, boreala myrmarker, vegetation, redox potential, klimatförändring

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1. Introduction

Climate change is an important and presently widely studied topic, with a lot of research conducted in this field. Increased carbon dioxide (CO_2) concentration in the atmosphere is a major driver of climate change and often mentioned when discussing climate change (Jiang et al. 2019). However, methane (CH_4) is another important driver of climate change and actually a much more powerful greenhouse. Methane is over 20 times more efficient at trapping heat than carbon dioxide (Lelieveld et al. 1998, IPCC 2014). Anthropogenic sources of methane include landfills and agriculture, but methane is also naturally produced in wetlands like boreal mires (Gorham 1991, Lelieveld et al. 1998). Even though boreal mires cover less than 3% of the world's total land area, it has been estimated that they store up to one-third of the world's soil carbon storages (Gorham 1991, Turunen et al. 2002). Thus, boreal mires are an important part of the global carbon cycle and major contributors to the global methane budget, and therefore they have to be considered when the effects of climate change are predicted. In particular since, it is known that there is large variability in methane fluxes and, driving factors behind this variability are not yet very well understood (eg. Limpens et al. 2008, Turetsky et al. 2014).

1.1 Carbon cycle of mires

Estimates from Finnish mires have shown that boreal mires have accumulated carbon during the Holocene (Turunen et al. 2002) and at present-day most mires are sinks of carbon (e.g. Nilsson et al. 2008). Whether a mire is a sink or a source of carbon depends on a delicate balance between production and consumption of CO_2 and CH_4 that are the two main parts of carbon cycling at peatlands (Silvola et al. 1996, Nilsson et al. 2008). Lateral transfer of carbon with groundwater also contributes to carbon cycling at mires (Nilsson et al. 2008).

1.1.1 Net ecosystem exchange

Net ecosystem exchange (NEE) describes the movement of CO_2 between an ecosystem and the atmosphere. NEE is the sum of production and consumption of CO_2 (Lindhrot et al. 2007, Aurela et al. 2001), both of which are tightly linked to vegetation and plants are therefore an important controller of NEE. Vegetation is important, especially when considering CO_2 consumption, where CO_2 is absorbed from the atmosphere by plants through photosynthesis. This uptake of CO_2 is called gross primary production (GPP) and it depicts the total amount of CO_2 bound to the vegetation (Aurela et al. 2001, Nilsson et al. 2008, Lund et al. 2010).

The other part of NEE is ecosystem respiration (R_{eco}) that includes processes in which CO_2 is released. Ecosystem respiration consists of two parts, autotrophic and heterotrophic respiration and thus includes all CO_2 released from an ecosystem through respiration (Lafleur et al. 2005, Lindhrot et al. 2007, Lund et al. 2010). Autotrophic respiration includes respiration from above-ground plant parts as well as respiration from roots beneath the peat surface (Lloyd & Taylor 1994, Aurela et al. 2001). Root respiration is, thus, considered a part of soil respiration together with the heterotrophic respiration, which is the respiration of the heterotrophic community in peat, mainly organisms that participate in decomposing dead organic material (Lloyd et al. 1998, Lafleur et al. 2005).

1.1.2 Methane flux

Methane flux is the balance between methane production and consumption, which carried out by different microorganisms in the peat. Methanogens that belong to the domain archaea are mainly responsible for methane production (Garcia et al. 2000, Whalen 2005). There are several species of methanogens, which together with other microorganisms, form a complex food web, through which dead organic material is anaerobically decomposed (Whalen 2005, Lai 2009).

The decomposing chain starts with hydrolytic and fermenting bacteria that begin the decomposing process by breaking down complex organic compound to simple ones, like alcohols, short-chain fatty acids, CO_2 and H_2 (Whalen 2005, Lai 2009). These products are then further used by methanogens to produce methane. Some methanogen species are able to utilize formate and methylene compounds, like methanol, to produce methane, but otherwise, methane is mainly produced through two primary pathways (Garcia et al. 2000, Whalen 2005). The first pathway is based on reduction and oxidation reactions in which H_2 is used as an electron donor and CO_2 acts as electron acceptor (Equation 1.). CO_2 is thus reduced in this reaction and the result is methane and water (Garcia et al. 2000, Whalen 2005, Lai 2009).

$$4H_2 + \mathrm{CO_2} \rightarrow \mathrm{CH_4} + 2\mathrm{H_2O}$$

Equation 1.

In the second pathway, acetate is broken down through fermentation into CH_4 and CO_2 (Equation 2.) (Garcia et al. 2000, Whalen 2005, Lai 2009). Methanogens therefore also contribute to soil respiration and in this way, play a role in CO_2 flux of peatlands.

$$CH_3COOH \rightarrow \mathrm{CO_2} + \mathrm{CH_4}$$

Equation 2.

Methanogens do not tolerate oxygen; in other words, they are obligate anaerobes (Garcia et al. 2000). Microbial methane production happens, therefore, mostly in the deeper part of the peat with limited oxygen concentration. The CO_2 reducing pathway is more dominant in the deeper part of the anaerobic peat layer, while the acetate pathway is more typical further up near the oxygenized uppermost peat layer (Hornibrook et al. 1997).

The oxygenized surface layer of the peat is where methane consumption primary takes place (Whalen 2005, Lai 2009), but an oxygenated layer in which methane is consumed is also created around plant roots especially when they are photosynthetically active (Lloyd et al. 1998). In the presence of oxygen, CH_4 is consumed by methanotrophs, belonging to the genus Eubacteria (Whalen 2005). This is achieved through oxidation of methane where oxygen is an important part and acts as an electron acceptor (Equation 3.) (Whalen 2005, Lai 2009). The end product of this oxidation chain is CO_2, which again links methane and CO_2 fluxes together.

$$\mathrm{CH_4} \rightarrow CH_3OH \rightarrow HCHO \rightarrow \mathrm{CO_2}$$

Equation 3.

Consumption of methane can, however, also occur in anaerobic conditions through reauction of iron, nitrate or sulfate, but the overall impact of anaerobic processes on methane consumption is smaller than aerobic oxidation of CH_4 (Kumaraswamy et al. 2001, Smemo & Yavitt 2011).

1.2 Variability of CH_4 flux

CH_4 fluxes from mires vary considerably both spatially and temporally (Bellisario et al. 1999, Limpens et al. 2008, Turetsky et al. 2014, Koebsch et al. 2015, Dinsmore et al. 2017, Marushchak et al. 2016). Some mires have been observed to function as net sinks of CH_4 (Granberg et al. 1997, Minkkinen & Laine 2006), but most studies report mires to be sources of CH_4 (Granberg et al. 1997, Nilsson et al. 2001, Christensen et al. 2003, Dinsmore et al. 2017). The magnitude of CH_4 flux changes with latitudes, where the CH_4 flux is generally higher from mires at low latitudes than from mires at higher latitudes, like boreal mires (Turetsky et al. 2014). Flux also differs between mire types, where nutrient-poor ombrotrophic bogs often have lower CH_4 flux than more nutrient-richer minerotrophic fens (Nykänen et al. 1998, Öquist & Svensson 2002, Nilsson et al. 2001).

Variation in the CH_4 flux can also occur within the same mire, as mires are not homogeneous habitats, but instead often mosaics of different surfaces with varying environmental conditions,

which leads to within mire spatial variation in CH_4 flux (Bubier 1995, Bergman et al. 1998, Marushchak et al. 2016). In addition, boreal mires occur at locations with varying environmental conditions between seasons and conditions also differ between years, which leads to temporal variation in the CH_4 flux both within and between years (Koebsch et al. 2015, Dinsmore et al. 2017).

Several factors have been linked to both spatial and temporal variation in the CH_4 flux. In laboratory conditions, methanogenesis has been determined to be sensitive to change in soil temperature (Dunfield et al. 1993, Bergman et al. 1998, Lloyd et al. 1998), but in field studies temperature has been able to explain variation in CH_4 flux to varying degrees (Granberg et al. 1997, Nykänen et al. 1998, Christensen et al. 2003). Nonetheless, temperature is still regarded as a major controller of CH_4 flux (Christensen et al. 2003, Koebsch et al. 2015, Dinsmore et al. 2017). Water table position (WTP) is another factor that is known to influence CH_4 flux. Water can act as a diffusion barrier for atmospheric oxygen and WTP, therefore, divides the peat into an aerobic and anaerobic layer (Öquist & Svensson 2002). Thus, it could be assumed, that when WTP is low more CH_4 is oxidized in the thicker aerobic layer, resulting in lower CH_4 flux. On the other hand, higher WTP could result in larger CH_4 flux due to a thinner aerobic layer where less CH_4 is oxidized and a thicker anaerobic layer where more CH_4 is produced. There is, however, contradicting evidence for the direction of correlation between WTP and CH_4 flux, with some studies indeed reporting positive correlations (e.g. Granberg et al. 1997, Strack et al. 2014), but other studies have found negative correlations (e.g. Bellisario et al. 1999, Dinsmore et al. 2017).

Likewise, vegetation composition can affect CH_4 flux in several ways. Primary production provides recently fixed carbon that is used by several groups of bacteria in peat, which in turn provide substrata from methanogenesis (Bergman et al. 1998, Joabsson et al. 1999, Bellisario et al. 1999, Öquist & Svensson 2002). Indeed, it has been shown that a large part of CH_4 released from mires is driven from recently fixed carbon (Bellisario et al. 1999). Connection of substrate availability and primary production to CH_4 flux has also been proven on large-scale with comparisons between mires and other methane-producing ecosystems from different regions (Whiting & Chanton 1993, Christensen et al. 2003). Another way by which vegetation can directly influence CH_4 flux is by transportation of CH_4 through plant tissues (Joabsson et al. 1999, Bellisario et al. 1999, Öquist & Svensson 2002). Especially sedges that have aerenchyma tissues, through which gases can easily

travel, have been shown to be important methane transportation pathways (Lloyd et al. 1998, Bellisario et al. 1999, Nilsson et al. 2001, Marushchak et al. 2016). CH_4 transport through plants can be passive diffusion between peat and the atmosphere or active transportation (bulk transportation) of CH_4, which is mediated by respiration of plants that create a consecration gradient (for example in temperature) between the atmosphere and plant tissue (Joabsson et al. 1999, Whalen 2005).

1.3 Reduction-oxidation potential

Reduction-oxidation (redox) potential describes the tendency of a chemical substance to either be reduced (gain electrons) or oxidized (lose electrons) (Jacob 1970). Redox potential is a relative measure by which values are compared to the reduction potential of a hydrogen (H) reference electrode with a redox potential of zero (unit V) (Paleo Terra 2020, Jacob 1970). Therefore, a positive redox potential indicates that a substance has a higher affinity to be reduced than hydrogen, whereas negative values indicate that the substrate has a lower affinity to be reduced, in other words, it will be oxygenized (Jacob 1970, Ponnamperuma 1972).

Highest redox potentials in soils are reached in the presence of oxygen (Wang et al. 1993, Lloyd et al. 1998, Yu et al. 2001). Since oxygen is highly reactive many chemical substances will be oxides in the presence of oxygen as they lose electrons to oxygen that acts as an electron acceptor (Ponnamperuma 1972). In waterlogged soil, like most mires, oxygen is often present only in the uppermost layer (that can be as thin as a few centimetres) (Lloyd et al. 1998). In the absence of oxygen other chemical substances with lower redox potential are used as electron acceptors. Common electron acceptors present in soils are nitrate (NO_3^-), manganese (Mn^{+4}), iron (Fe^{+3}), sulphate (SO_4^{-2}) and carbon dioxide (CO_2) (Ponnamperuma 1972, Peters & Conrad 1996, Yao et al. 1999, Gao et al 2002). Furthermore, humic acids in soil have been shown to participate in redox processes (Struyk & Sposito 2001, Lipson et al. 2010). Reduction of electron acceptors in soil follows a sequence where after oxygen, first NO_3^-, then Mn^{+4}, Fe^{+3}, SO_4^{-2} and lastly CO_2 is reduced. This sequence follows the redox potential of electron acceptors form the highest potential of NO_3^- to the lowest potential of CO_2 (Ponnamperuma 1972, Peters & Conrad 1996, Yao et al. 1999). Redox potential of soil can, therefore, indicate which chemical substance is primarily used as an electron acceptor. However, in practice, several electron acceptors can be used simultaneously (Peters & Conrad 1996, Yao et al. 1999, Gao et al. 2002), which makes measured redox potential a

combination of potential of several electron acceptors. Nonetheless, redox potential measurements give an indication of which reactions are dominating in the ground and which processes are likely to be active.

Electron acceptors, that are higher up in reduction chain than CO_2 (alternative electron acceptors), provide thermodynamically more favourable metabolic pathways than reduction of CO_2. Therefore, in the presence of alternative electron acceptors methanogen would be outcompeted, which suppresses methane production (Peters & Conrad 1996, Teh et al. 2008, Knorr et al. 2009). This means that methanogenesis occurs in highly reducing condition where most other electron acceptors already have been reduced, a situation which causes a low redox potential (Wang et al. 1993, Yao et al. 1999, Yu et al. 2001). Therefore, redox potential could reflect whether conditions are suitable for CH_4 production or consumption, which would make redox potential a useful indicator of CH_4 flux.

1.4 Research questions

Understanding both spatial and temporal variation in CH_4 flux is important to identify the driving factors behind variation in CH_4 flux. This, in turn, helps to predict how boreal mires will affect climate change and how climate change in the future will affect the methane cycle of these mires. In this thesis, I seek to identify if small-scale spatial variation in the CH_4 flux occurs within the studied mire area. In addition, I strive to identify important drivers of the observed spatiotemporal variation in CH_4 flux during the summer, with a specific focus on the effect of vegetation properties and redox potentials on CH_4 flux.

Research questions thus are:

1. Is there spatial small-scale variation in the methane fluxes within the mire ecosystem?
2. Which environmental factors can explain spatiotemporal variation in methane fluxes over the growing season?
    a) Does gross categorizing into vegetation types provide a good basis for explaining CH_4 flux or is more detailed information of individual plant functional types needed?
    b) Can redox potential provide an additional parameter to use when predicting CH_4 flux?
    c) Which other environmental variables are important when predicting CH_4 flux?

2. Materials and methods

2.1 Study site

The study site is located in Sodankylä at a boreal fen, Halssiaapa (67°22'06.6"N 26°39'16.0"E), in northern Finland, about 7 kilometres south of Sodankylä city centre near the Arctic Research Center of the Finnish Meteorological Institute (Fig. 1 a and b). Halssiaapa is classified as a eutrophic fen, with an open, mostly treeless landscape (Hyvönen 2015, Dinsmore et al. 2017). The vegetation transitions from open fen to tree-covered mire at the edges of the fen. The open fen has a surface structure consisting of drier string, wet flarks and intermediate surfaces (lawns) between the two (Hyvönen 2015, Dinsmore et al. 2017). Strings are slightly higher than the surrounding landscape and covered mostly by sphagnum mosses. Another typical characteristic of strings is the presence of shrubs (like *Betula nana*, *Andromeda polifolia* and *Vaccinium oxycoccos*). Flarks, on the other hand, are mostly dominated by mosses thriving in wet conditions (like *Sarmentypnum* sp.) and species from *Carex* and *Eriophorum* geniuses. This is due to flarks having a high WTP that can rise above the peat surface. Intermediate surfaces are a mix between string and flarks in both vegetation characteristic and WTP. Some intermediate surfaces are also almost completely covered by sphagnum mosses (sphagnum lawns) (Hyvönen 2015, Dinsmore et al. 2017, Räsänen et al. 2019).

Long-term CO_2 and CH_4 flows have been measured at Halssiaapa with the eddy covariance method since 2011 (Finish Meteorological Institute, 2019). In the surrounding area of the eddy covariance tower, three measurement clusters with three measurement plots each were established in 30 of April 2019. In total there were nine measurement plots, of which three were situated on flarks (Flark_1, Flark_2 and Flark_3), three on lawns (Lawn_1, Lawn _2 and Lawn _3) and three on strings (String_1, String _2 and String _3) (Fig. 1 c) (See appendix fig. 1 for pictures of all measurement plots). A rectangular metal collar (60 cm x 60 cm) (Fig. 1 d) was installed to each measurement plot. Furthermore, a redox-potential measurement device was installed at each of the clusters with one sensor for every measurement plot. All measurement clusters and plots were accessible by boardwalks, which minimized disturbance to vegetation and the fen surface.

Figure 1. a) Location of the study (orthophotograph from Paituli: https://avaa.tdata.fi/web/paituli/latauspalvelu). b) Location of Sodankylä in Finland (Google maps). c) Drone picture (drone pilot Kari Mäenpää and the picture was processed by Aleksi Räsänen) of the study area (Picture was taken on 12.7.2016). Red circles represent string plots (String_1, String _2 and String _3), purple circles lawn plots (Lawn_1, Lawn _2 and Lawn _3) and blue circles flark plots (Flark_1, Flark_2 and Flark_3). The eddy covariance tower is connected to a small booth where measurement instrument (including the PICARRO CO_2 and CH_4 analyzer) are situated. d) Example of measurement plot setup (Flark_3, picture was taken on 17.7.2019).

2.2 Field measurements

2.2.1 CO_2 and CH_4 flux measurements

The closed chamber technique is used to acquire small-scale CO_2 and CH_4 flux measurements. This makes it possible to obtain measurements of gas fluxes from specific vegetation communities, in contrast to the eddy covariance method that provides an overview of gas fluxes of the surrounding fen area as a whole (Griffis et al. 2000). CO_2 and CH_4 flux measurements were taken at each study plot by placing a chamber onto the metal collar, with water poured into the collar to ensure that the chamber is airtight. Each measurement lasted from 3 to 5 minutes and between measurements the chamber was ventilated for 1 to 2 minutes. Change in CO_2 and CH_4 concentration was measured with a PICARRO (Picarro Inc., Santa Clara, USA) CO_2 and CH_4 analyzer that was connected to the chamber by a plastic tube. Inside the chamber, the air was circulated by a small fan to ensure that gas concentrations remained homogenous throughout the chamber during measurements.

Two different chambers (Fig. 2 a and b) were used for gas flux measurement. An opaque metal chamber was used to obtain measurements in total darkness. To capture the influence of photosynthetic capacity, measurements were also carried out with a transparent chamber made from plexiglass. The bottom area of both used chambers was 0.36 m^2 and the heights were 30 cm and 40 cm for the opaque chamber and the transparent chamber, respectively. The chamber volumes were, thus, 0.108 m^3 for the opaque chamber and 0.144 m^3 for the transparent chamber.

Transparent chamber measurements were taken, if possible, during sunny days. Measurements were taken in full sunlight (without any shading) and in 1 - 3 different shading levels. Shading was created with nets that were stretched over a wooden frame. These nets were then placed on top of the chamber to cast a shadow over the measured area (Fig. 2 c). Photosynthetically active radiation was measured in PAR with PQS1 PAR Quantum Sensor (KIPP & ZONE). Radiation measurements (as PAR in mV that was later converted to $\mu mol/m^2s$) were taken from outside of the chamber by placing the instrument at a corner of the chamber.

During chamber measurements temperature inside the chamber, soil temperature (from a depth of 8 cm) and water table position (WTP) were measured. WTP was measured as distance (cm) from the upper edge of the metal collar from a plastic tube, with small holes, that was immersed

in the peat. Negative values indicated water table position below the metal collar and positive values that the WTP was above the collar.

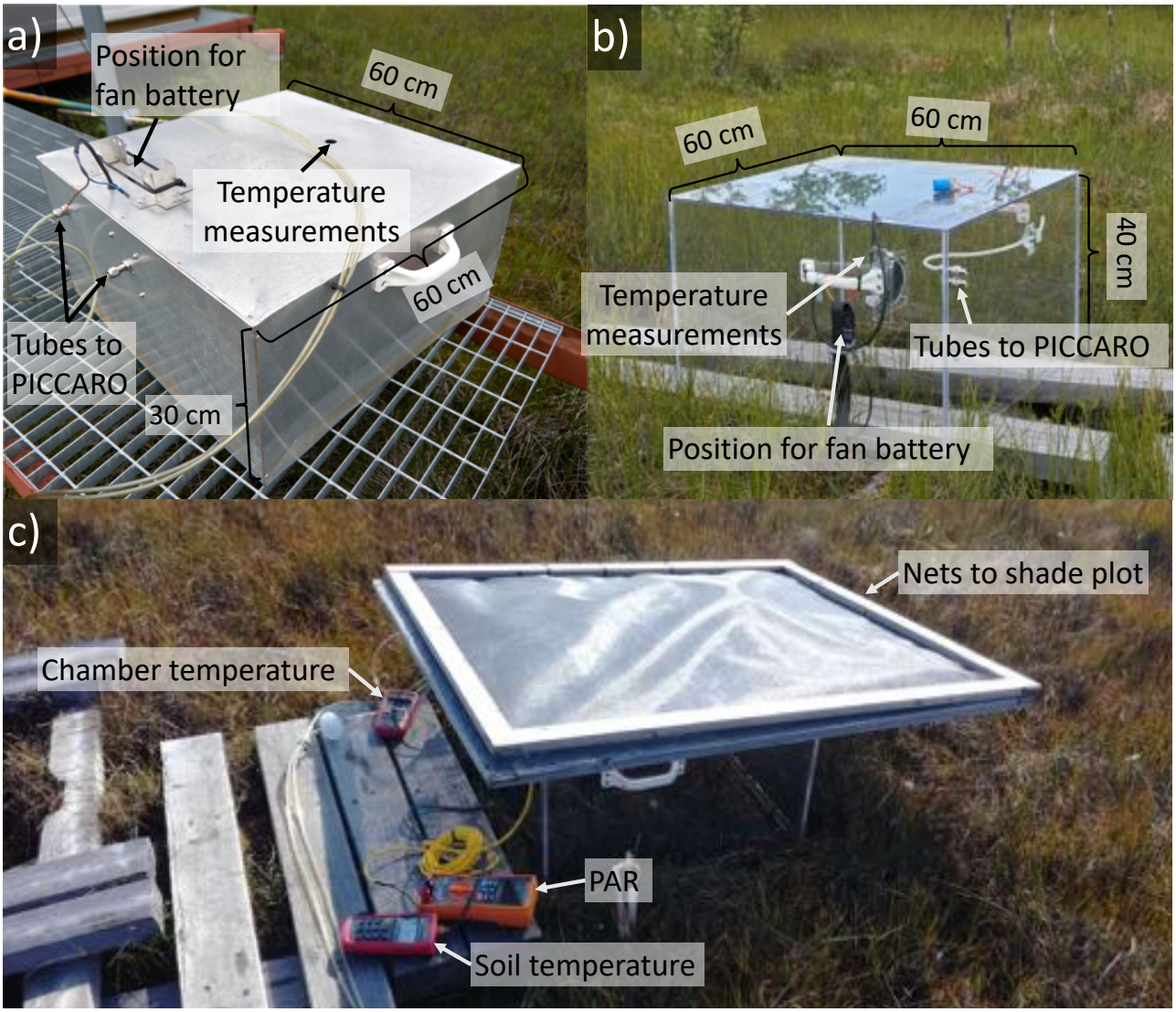

Figure 2. Picture of a) opaque and b) transparent chamber, as well as c) picture of how shaded transparent chamber measurements were taken. The measurement plot is Flark_2.

Chamber measurements were carried out during the time span of 24.06.2019-24.09.2019. Opaque chamber measurements were strived to be performed each weekday (5 times a week), but the actual number of measurement times varied weekly. Transparent chamber measurements were conducted about once a week, if possible, on a sunny day to ensure good light conditions (See appendix table 1 for a list of measurement dates).

2.2.2 Redox potential

At each measurement cluster, one redox potential instrument (Paleo Terra, Amsterdam, Netherlands) was installed on the 30.05.2019. Each device consists of three probes with four platinum electrodes placed near the individual measurement plots, one reference electrode and a datalogger. Redox potential was measured in mill volts (mV) as the difference between the voltage at the sensing electrode compared to the voltage of the reference electrode. Since hydrogen electrodes are not optimal for field use, a silver-silver chloride electrode (Ag-AgCl) was used as the reference electrode. The device produces continuous measurements of redox potential with 15-minute intervals from four depths (5, 15, 25 and 40 cm form peat surface).

Values derived by using an Ag-AgCl reference electrode require a correction factor to be comparable to the standard Eh values, obtained by using a hydrogen reference electrode. A + 200 mV correction is thus added to measured values to reach the standard Eh values. Furthermore, redox data was pH corrected by adding 59*(pH-7) mV to the observed redox values. Measurements of pH were performed by Juha Mikola in summer of 2016 at locations around the study area. The exact pH measurement points did not match the chamber measurement plots, and therefore the closest pH measurement from corresponding vegetation type was used.

2.2.3 Additional data

Information about coverage of plant species as well as dead organic matter (litter) at measurement plots was estimated by vegetation surveys done at the fen during the summer. Vegetation surveys were carried out with approximately two weak intervals by Viivi Lindholm (See appendix table 2 for list of measuring times). Vegetation survey data was extended to the end of the measurement period by estimating plant coverage from photographs of measurement plot at the last measurement day.

Long-term meteorological data for the area was obtained from the Finish meteorological institute. Meteorological measurements used in this work were air temperature at 3 m, PAR ($\mu mol/m^2s$), relative humidity (%) and precipitation (mm).

2.3 Variable calculations

2.3.1 CH_4 and CO_2 flux

The principle of flux calculations is to record the change in gas concentrations in a closed chamber and use the slope of concentration change to calculate the amount and direction of gas flux between the ecosystem and the atmosphere. Fluxes for both carbon dioxide and methane were calculated with the formula modified from Duc *et al.* (2013):

$$F = \frac{SlopePV}{RTA}$$

Equation 4.

Here F is gas flux (μmol m^{-2} s^{-1}), slope represents the accumulation of gas (CO_2 or CH_4) over time (μmol mol^{-1} s^{-1}), P is atmospheric pressure at the time of measurements (atm), V is chamber volume (mL), R is a gas constant (82.0562 mL atm K^{-1} mol^{-1}), T is chamber temperature (K) and A is measurement area (m^2). The slope was calculated as a linear fit to the measured gas concentration during individual chamber measurement. Flux values derived from the equation are in the unit of μmol m^{-2} s^{-1}. The molecular weight of each of the gasses (44u for CO_2 and 16u for CH_4) were used to get the final units of mgCO_2 m^{-2} s^{-1} and μgCH_4 m^{-2} s^{-1} for CO_2 and CH_4 respectively. Negative flux values indicate that the measured gas is bound to the plot and positive values indicate the release of gas to the atmosphere.

Leaking of the chamber or other problems during measurements can cause gas concentration to rise non-linearly. These measurements were removed by discarding measurements where R^2 value of slope fit was under 0.99 for CH_4 as well as for CO_2 flux measurement with the opaque chamber. Varying light conditions during measurements can affect the accumulation of CO_2 in the transparent chamber and thus the limit of R^2 was lowered to 0.8 for measurements where PAR was over 430 μmol $m^{-2}s^{-1}$. Rejection limit of 0.5 was used for CO_2 flux in the transparent chamber when PAR was lower than 430 μmol $m^{-2}s^{-1}$. During these measurements change in CO_2 concentration was small, which in itself resulted in lower R^2 values. Furthermore, for CH_4 measurements with concentration increasing particularly fast, as compared to other measurements during the same day, were also removed, since the rise in CH_4 was likely due to eruptions of methane bubbles.

Flux calculations were performed with Microsoft Excel (version 16.20) and R^2 values for slopes were calculated with RStudio (Version 1.2.5001).

2.3.2 Gros primary production

Photosynthetic activity at different light intensities was estimated by calculating a light response curve. The light response curve was determined for each measurement plot based on calculated CO_2 flux for days with light and dark chamber measurements. Calculations were based on the Michaelis–Menten (rectangular hyperbola) light response curve (Equation 5) (Falge et al. 2001, Aurela et al. 2002):

$$GPP = \frac{\alpha * GPP_{max} * PAR}{GPP_{max} + \alpha * PAR}$$

Equation 5.

In the formula PAR is the measured photosynthetically active radiation (μmol/m^2s) during the transparent chamber measurement, α is the slope of the light response curve when PAR is close to zero, GPP_{max} is the maximal primary production capacity of the vegetation and GPP represents the actual gross primary production (i.e. the amount of CO_2 bound by vegetation) at the measurement time. GPP was not measured directly since CO_2 flux measurements of the transparent chamber represent the net ecosystem exchange (NEE). To calculate GPP the amount of respiration is removed from measured transparent chamber flux values. Respiration was determined as the amount of CO_2 released during opaque chamber measurement. Measurements used to calculate respiration were always taken the same day as the transparent chamber measurement in question. At some days more than one opaque chamber measurement was available and, in these cases, respiration was determined as the average of these fluxes.

Unknown parameters (α and GPP_{max}) of the GPP equation were estimated with Levenberg-Marquardt algorithm (function nlsLM from package minpack.lm in R). For GPP_{max} the range of possible values was set at 0 to -1 and α from -0.01 to 0.01 to get the model curve to follow a typical form of a light response curve. Estimation of parameters was performed for every day with transparent chamber measurements. For reliable calculation of light response, a minimum of two measurements from the transparent chamber were needed. By inputting estimated α and GPP_{max} and setting PAR as 1200 μmol/m^2s GPP at PAR of 1200 μmol/m^2s was calculated (GPP_{1200}) to represent photosynthetic activity. Values of GPP_{1200} were then interpolated (linear interpolation) separately for each measurement plot to cover all measurement days.

2.3.3 Vegetation properties

Vegetation survey data was used to obtain information about the vegetation community at each measurement plot. Plant species were grouped into six functional groups; shrubs, forbs, graminoids, *Sphagnum* mosses, wet mosses and dry mosses (See appendix table 3 for list of species included in functional groups). Surface covered by litter constituted one additional group. Leaf area indexes (LAI) was calculated for shrubs, forbs and graminoids with formulas provided by Hyvönen (2015) (Table 1). For species that did not have an LAI formula, the formula of a species with the most similar growth pattern was used. For mosses *(Sphagnum*-mosses, dry mosses and wet mosses) and litter scaled coverage was used instead of LAI. The scaled coverage was calculated by dividing the coverage of the group with the total documented plant coverage for that plot. Total vascular plant LAI and moss coverages were also calculated. LAI and moss coverage variables were interpolated by linear interpolation to get values for all chamber measurement dates.

Table 1. Equations used to calculate LAI. P stand for plant coverage in percentage and K for mean plant height. The table is from Hyvönen (2015).

Functional group	Equation	r^2	Observations (n)
Carex sp. and *Scheuchzeria palustris*	$0.00653 * P$	0.92	48
Andromeda polifolia	$0.00705 * P$	0.91	48
Vaccinium oxycoccos	$0.0312 * \sqrt{P}$	0.92	31
Menyanthes trifoliata	$0.000215 * P^2 + 0.000562 * K^2$	0.91	24
Comarum palustre	$0.000774 * P^2$	0.93	12
Betula nana	$0.000146 * P^2 + 0.000105 * K^2$	0.97	10

2.4 Statistics

2.4.1 Spatial variation in CH_4 flux

Variance analyses (one-way ANOVA) was used to explore spatial variation in CH_4 flux for vegetation types and plots. To assess how much of the observed variation each grouping variable (vegetation type and measurement plot) explained, an R^2 value was calculated with a simper linear regression model (lm function in R). In the model, the grouping variable was set as the independent variable and CH_4 flux as the dependent variable. Comparison between individual groups was also performed (Tukey HSD). A significance level of <0.05 was used in all tests. Statistical tests and modelling were performed in RStudio (Version 1.2.5001)

2.4.2 Variable selection

For modelling, data was modified so that for each plot, a daily average was calculated for all variables. Respiration was calculated using only dark chamber measurement. For CH_4 flux and other variables, both dark and light chamber measurements were used. Variables used in modelling were vegetation variables, redox potential from all depths and environmental variables that included observed respiration (R_{eco}), GPP_{1200}, soil, chamber and air temperatures, water table position (WTP), relative humidity (RH), PAR and precipitation (Appendix table 4). Correlation between variables was explored and if the correlation between two variables was higher than 0.7 (or lower than -0.7), only one of the variables was chosen to be used in modelling.

2.4.3 Modelling

Generalized additive models (GAM) (function gam form package mgcv in R) was used to model connections between CH_4 flux and other variables. In GAM a smoother term is used for describing relationships between the response and independent variables. The smoother is defined as a spline that allows a nonlinear response curve to be fit to data (Hastie & Tibshirani 1986). For the independent variables in the model a low rank isotropic smoother, that is based on a thin plane spline and where null space was penalized so that a term could be dropped to zero, was used. For measurement plot, a smooth term intended for random variables was used (Wood). The model was run with Restricted maximum likelihood (REML) method. CH_4 flux was log-transformed due to right-skewed data.

To determine the best combination of vegetation properties to use in modelling, five initial models (Table 2) were tested. From these five initial models, the best fitting model was chosen based on AIC and R^2 values. Importance of variables in the best model was determined by removing one variable at a time from the model. The form of the smoothing term was transferred from the original model to the reduced model keeping the form of the smoothing term stable. The change in adjusted R^2 value was then recorded and compared to the R^2 value of the full model. Loss of explanation power by each variable was then used as a proxy for the importance of the variables to the model. Due to interaction among the remaining variables in the model, the given loss of explanatory power does not reflect the true variance explained of a variable in the full model. This is because the remaining variables in the model can compensate for the effect of the removed

variable due to cross-correlations of the variables. Therefore, the given numbers were treated as relative values to assess which variable had the largest effect compared to other variables.

Table 2. The five initial models used to determine which combination of vegetation properties provides the best model.

Model	Vegetation parameter
Model 1	Shrubs, forbs, graminoids, *Sphagnum*, dry and wet mosses and litter
Model 2	Vascular plant LAI, moss cover and litter
Model 3	Shrubs, forbs, graminoids, moss cover and litter
Model 4	Vascular plant LAI, *Sphagnum*, dry and wet mosses and litter
Model 5	Vegetation categories (flark, lawn and string)

2.4.4 Temporal autocorrelation

Due to the nature of collected data, with several repeated measurements from subsequent days, temporal autocorrelation of data points is likely. The effect of autocorrelation on the constructed model was assessed by plotting an autocorrelation plot (acf function in r) that reveals the percentage of autocorrelation for a number of time lags. Autocorrelation was not added as a structure to the model, as several of the measured variables were expected to have a seasonal change in values, which reflect autocorrelation, and so this addition could have complicated correct interpretations from the analyses.

3. Results

3.1 Environmental variables

Overall mean temperatures during the summer (11.4 ˚C for June, 14.4 ˚C for July, 11.5 ˚C for August and 7.1 ˚C for September) were close to long-term averages for the period of 1981 - 2010 (12.3 ˚C for June, 13.3 ˚C for July, 12.1 ˚C for August and 6.1 ˚C for September) (Fig. 3) (Finnish Meteorological Institute 2020). At the end of July, temperatures reached their highest point (27.9 ˚C for air, 33.3 ˚C for chamber and 20.8 ˚C for soil) and this period was clearly warmer than the rest of the growing season (Fig. 4). Lowest temperatures were observed at the end of September (-1.2 ˚C for air, 4.2 ˚C for chamber and 3.3 ˚C for soil) (Fig. 4). Note that temperatures in Fig. 4 were measured only during the flux measurements so these values represent daytime conditions. Mean temperatures over the summer were 13.1 ± 0.17 ˚C for air, 17.9 ± 0.17 ˚C for chamber and 12.8 ± 0.10 ˚C for soil temperature.

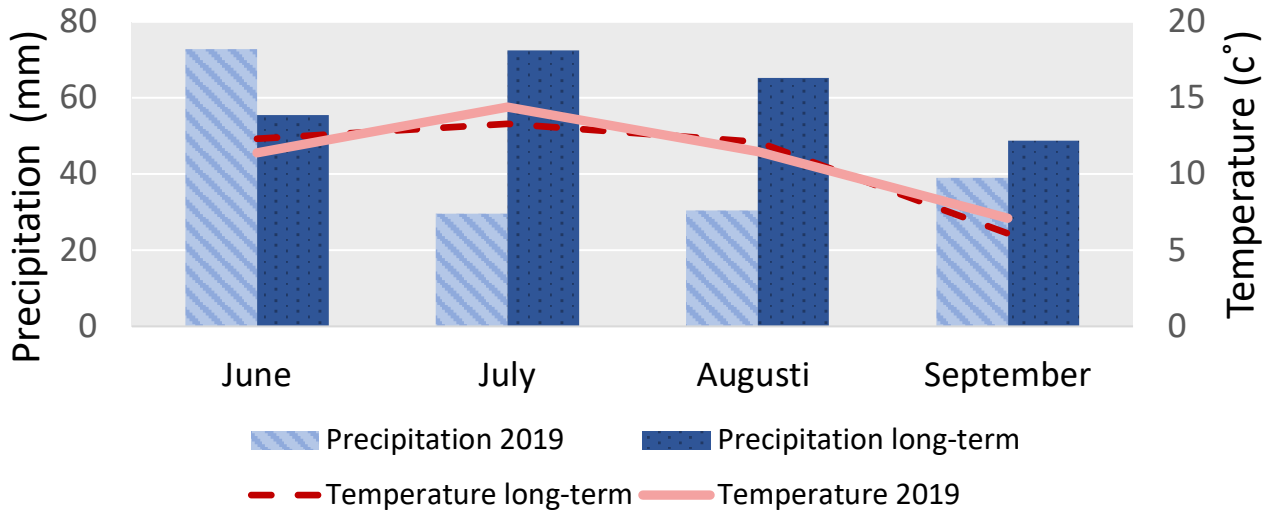

Figure 3. Mean monthly temperature and precipitation for the growing season of 2019 and long-term averages for the time span of 1981 to 2010.

Precipitation in June (72.9 mm) was higher than the long-term average (55.5 mm). July (29.6 mm) and August (30.5 mm) were on the other hand much dryer than the long-term averages (72.5 mm for July and 65.3 mm August) and precipitation of 39.1 mm in September was closer, but still under, the long-term average of 48.7 mm (Fig. 4) (Finnish Meteorological Institute 2020) (Fig. 4). Highest daily precipitation of 6.8 mm was observed on the first day of July. Average precipitation was 0.6 ± 0.04. Highest and smallest RH were 96.9 % and 31.9 % respectively with an average of 69.4 ± 0.47 %.

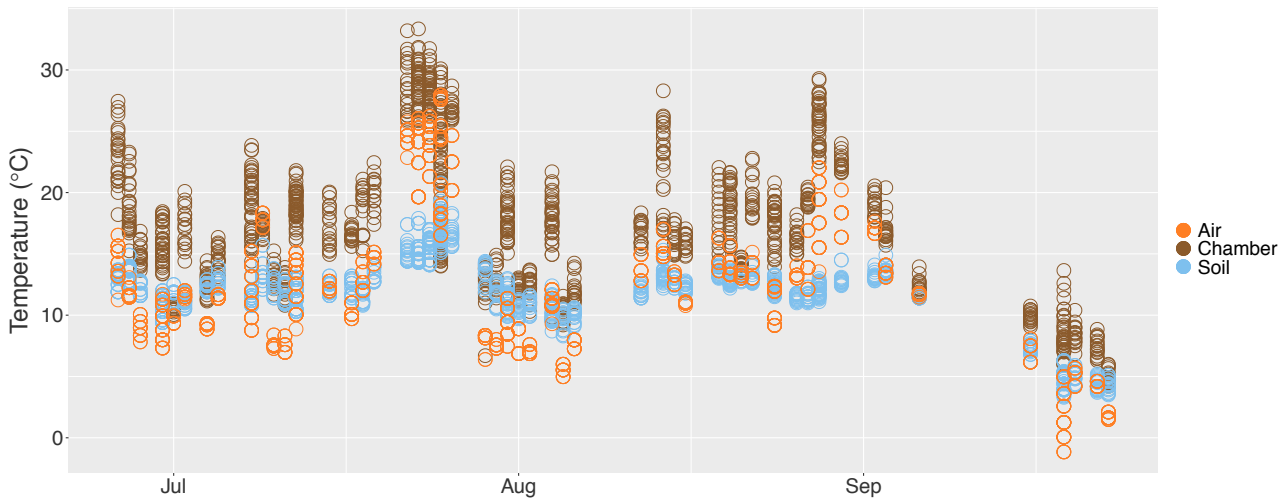

Figure 4. Observed air, chamber and soil temperature during chamber measurements.

WTP was at its highest at the beginning of the measurement period and decreased during July with about 10 cm. This decrease of WTP coincided with low precipitation in July and August. In mid-August to September WTP remained relatively stable (Fig. 5). WTP differed significantly between vegetation groups ($F = 1924$, $p < 0.001$), and explained 75 % ($r^2 = 0.753$) of variation in WTP. Measurement plot explained only slightly more of the observed variation ($r^2 = 0.783$, $F = 566.1$, $p < 0.001$). Highest water table level was recorded at Flark_2 (3.1 cm), but the other flark plots did not have drastically lower water levels. The lowest water table level was found in strings where String_2 had the lowest level of -35.5 cm. Average WTP was -5.0 $\pm$ 0.22 for flarks, 12.0 $\pm$ 0.20 for lawns, -25.0 $\pm$ 0.27 for strings and -13.9 $\pm$ 0.27 for the whole study area (See appendix table 5).

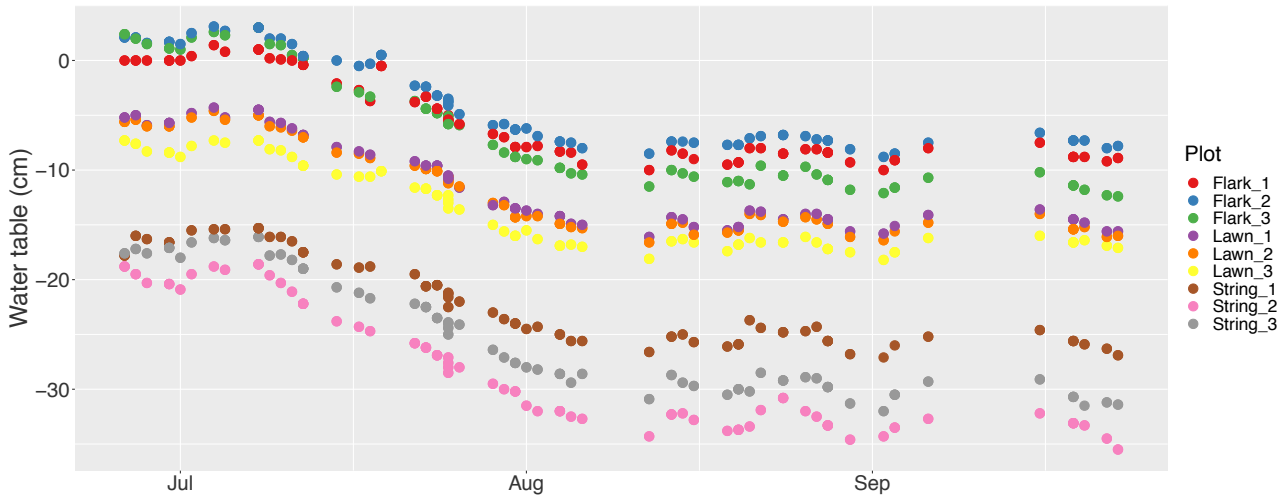

Figure 5. Measured WTP over the study period.

3.2 Redox potential

Redox potential was in general lower at the deeper peat layers and higher near the surface. The lowest potential of -316.7 mV was recorded from Lawn_2 at 40 cm, whereas the highest potential of 751.30 was recorded from String_3 at 5 cm. Average values of redox potential follow the depth with the highest average at 5 cm and lowest at 40 cm (Table 3), but for individual plots, redox potential was not always highest at the surface and lowest deeper down (Fig. 6). Redox potential at the surface shows the largest fluctuation in values, whereas in deeper layers it was relatively stable throughout the study period.

Table 3. Minimum and maximum values for redox potential at each depth and average value with standard error.

Depth	Minimum	Maximum	Average
5 cm	-292.7	751.3	56.1 ± 11.0
15 cm	-285.0	712.0	-151.7 ± 7.3
25 cm	-303.8	-55.7	-228.0 ± 1.1
40 cm	-316.7	-163.7	-238.6 ± 0.9

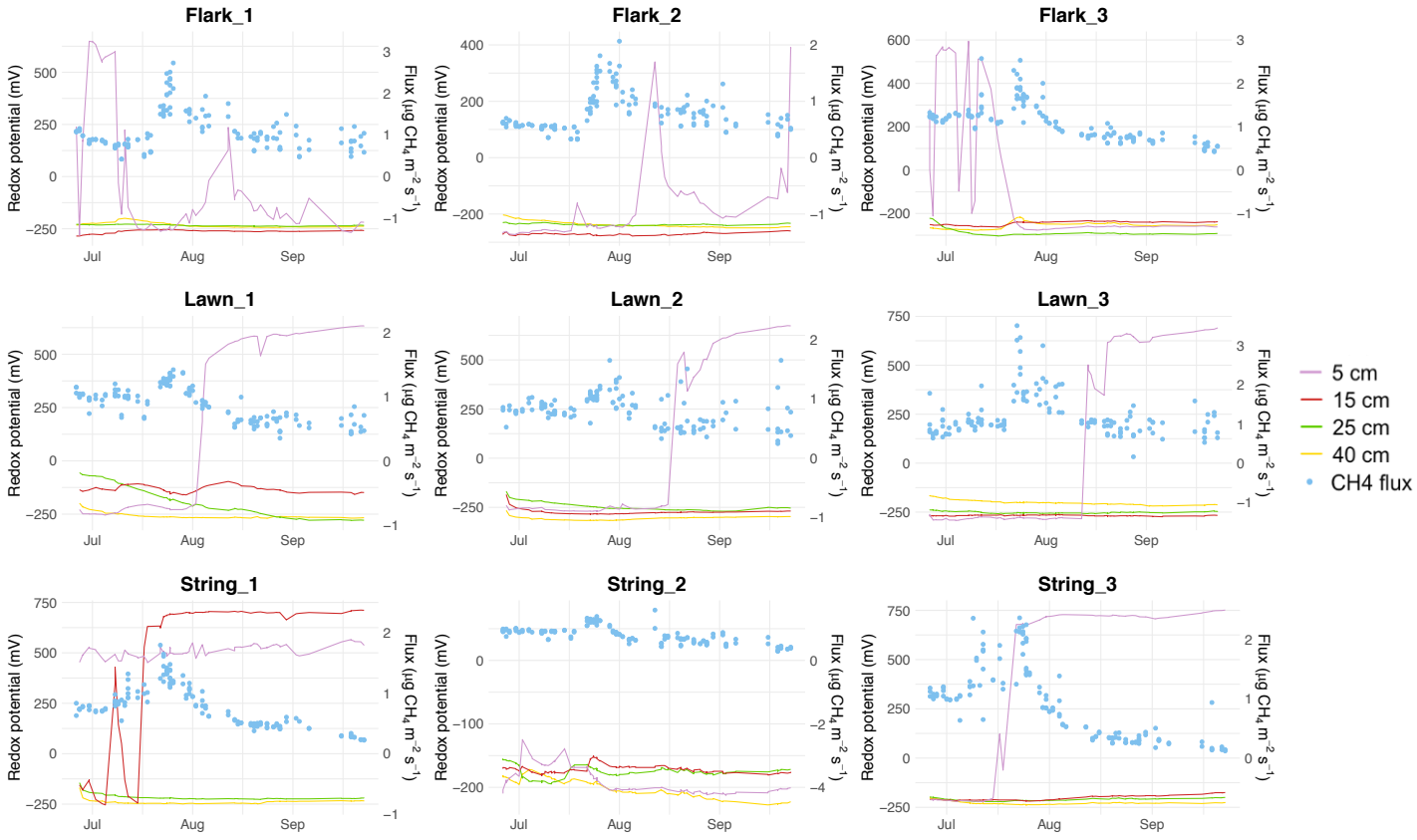

Figure 6. Change in redox potential from all depths and methane flux for individual measurement plot over the study period.

Variation in redox potential for all depths was statistically significant between both vegetation types and measurement plots (Table 4). In pair-ways comparison between plots, redox potential at 40 cm differed significantly for almost all plots. Moving closer to the surface, more plots were similar in their redox potential (Appendix table 8). Vegetation type explained less of the observed variation in redox potential (R^2 from 0.143 to 0.283) than measurement plot (R^2 from 0.375 to 0.862). When vegetation type was used as grouping variable R^2 was lowest for redox potential at 5 cm and 40 cm, where vegetation type explained 14 % of the variation. Measurement plot as grouping variable explained well the variation in redox potential at 40 cm, but R^2 values were high also for the depths 25 cm and 15 cm. For redox potential near the surface, plot explained 38 % of the measured variation.

Table 4. ANOVA result for redox potential at all depths (5, 15, 25 and 40 cm) with both plot and vegetation type as a grouping factor.

Depth	Group	R^2	F	P
Redox 40 cm	Vegetation	0.143	104.2	<2e-16
Redox 25 cm	Vegetation	0.283	246	<2e-16
Redox 15 cm	Vegetation	0.261	219.6	<2e-16
Redox 5 cm	Vegetation	0.143	104	<2e-16
Redox 40 cm	Plot	0.862	967.7	<2e-16
Redox 25 cm	Plot	0.635	269.6	<2e-16
Redox 15 cm	Plot	0.803	632.3	<2e-16
Redox 5 cm	Plot	0.375	92.75	<2e-16

3.3 Vegetation

Overall vegetation properties of individual plots were as expected based on their assigned vegetation community type (Fig. 7). Wet mosses were the only moss group present at flarks, whereas strings were mostly *Sphagnum* dominated with some smaller occurrence of dry mosses. In lawn plots all three moss functional groups were present, and at lawn_3 they even co-occurred on the same plot. Therefore, lawns were, as expected, a mix between flarks and strings. Furthermore, *Sphagnum* was the dominating moss in Lawn_3, where almost the whole plot was cover with *Sphagnum*. Graminoids were found in all plots, with the largest occurrence in Flark_2. Forbs occurred at all three vegetation types but were not present on all plots. In fact, Flark_3 was the only flark plot where forbs were present and here only the species *Scheuchzeria palustris* occurred. Shrubs were found only at strings and lawn plots one and two, with greatest occurrences on strings.

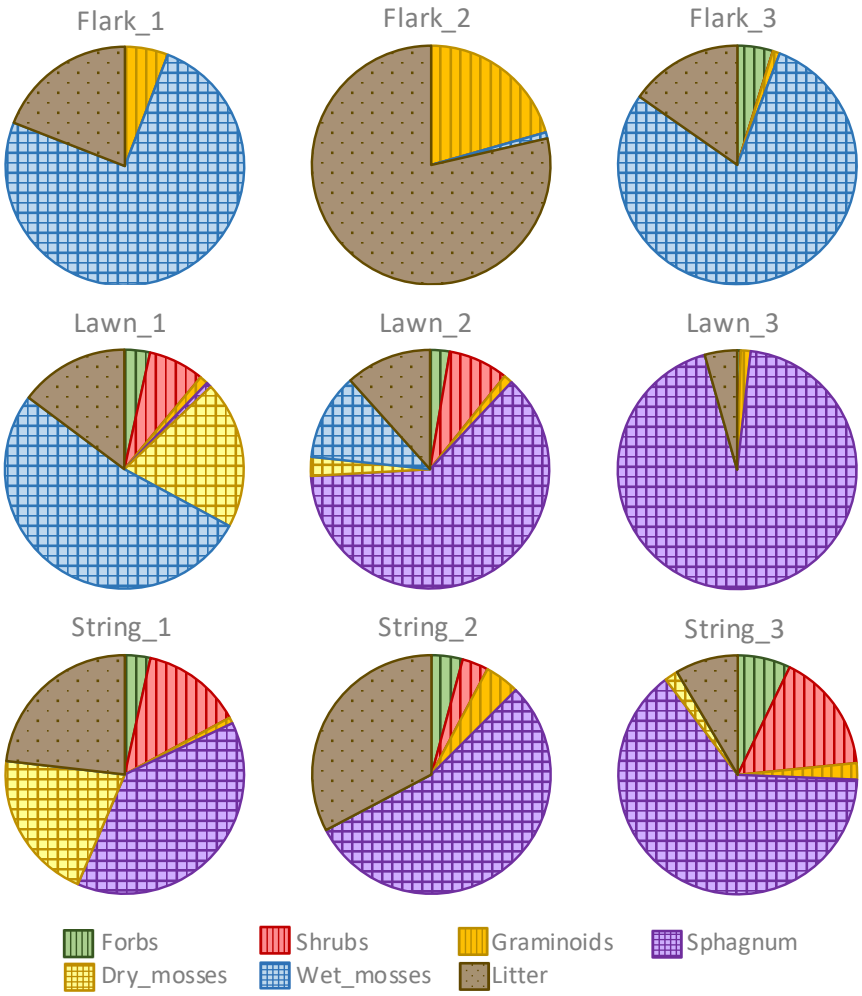

Figure 7. Pie chart describing the vegetation composition of each measurement plot. Note that vascular plants are LAI values and mosses and litter are coverages. The charts sill roughly describes the proportions of each functional group.

3.4. Gas fluxes

Highest CH_4 flux (3.51 μg CH_4 m^{-2} s^{-1}) was recorded during the warm period in July and lowest flux (0.12 μg CH_4 m^{-2} s^{-1}) was observed in September, at the end of the measurement period (Fig. 8 a). Mean CH_4 flux over measurement period was 0.94 ± 0.01 μg CH_4 m^{-2} s^{-1}. There was no significant difference between CH_4 flux from dark and light chambers (F = 0.195, P = 0.659). Respiration follows a similar pattern (Fig. 8 b) as the CH_4 flux. Highest and lowest respiration were 0.41 mg CO_2 m^{-2} s^{-1} and 0.02 mg CO_2 m^{-2} s^{-1} respectively, with mean respiration being 0.11 ± 0.002 mg CO_2 m^{-2} s^{-1}. Calculated uptake of CO_2 at PPFD 1200 (GPP_{1200}) varied between 0.48 mg CO_2 m^{-2} s^{-1} and 0.02 mg CO_2 m^{-2} s^{-1}, with the mean of 0.21 ± 0.003 mg CO_2 m^{-2} s^{-1}. GPP_{1200} was highest at the beginning of the measurement period and started to decrease in late August (Fig. 8 c). This indicates that the very beginning of the growing season was not captured by measurements.

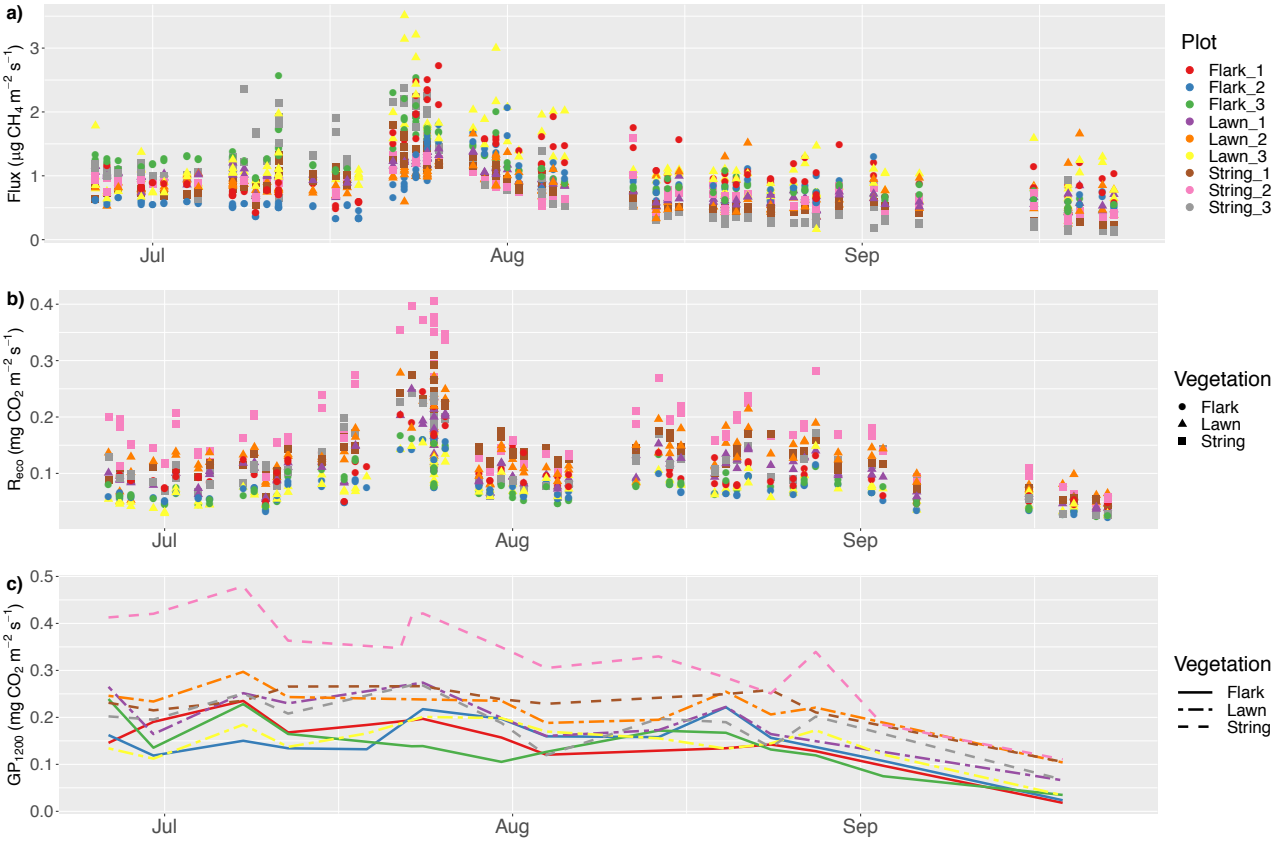

Figure 8. Development of measured (a) CH_4 and (b) CO_2 fluxes as well as calculated (c) GPP_{1200} values over the measurement period. Measurement plots are indicated by colours and vegetation type by the shape of the points or line type.

Variation in CH_4 flux was significant between vegetation types (F = 14.29, P > 0.001), but this was true only for strings smaller CH_4 fluxes than those observed for flarks (p > 0.001) and lawns (p > 0.001) (Fig. 9 b). Furthermore, vegetation type explained only 2 % (r^2 = 0.023) of variation in CH_4 flux. Measurement plot, on the other hand, explained 12 % (r^2 = 0.115, F = 19.7, P > 0.001) of variation in CH_4 flux. However, comparison between all measurement plot revealed that most plots had similar CH_4 fluxes and the only plots which differed from other plots were Flark_1, Flark_3 and Lawn_3 (Fig. 9 a) (Appendix, Table 7).

Vegetation types differ from each other also in R_{eco} (F = 88.75, P < 0.001), with highest respiration in string and lowest in flarks (Fig. 9 d). Vegetation type explained 18 % (r^2 = 0.175) and plot 5 % (r^2 = 0.052, F = 48.14, P > 0.001) of variation in R_{eco}. There was, however, deviation between plots form the same vegetation type and some plot from different vegetation types did not differ in R_{eco} (Fig. 9 c) (Appendix, Table 7). GPP_{1200} also differed between vegetation types (F = 290.4, P > 0.001) with highest values in strings and lowest in flarks (Fig. 9 f). Comparison of variance between plots (F = 212.6, P > 0.001), revel larger differences (Fig. 9 e) than for CH_4 flux or respiration. String_3

differed from all other plots (Appendix, Table 7) and had the largest GPP_{1200} values. Vegetation type explained 33 % (r^2 = 0.325) and plot 59 % (r^2 = 0.586) of variation in respiration.

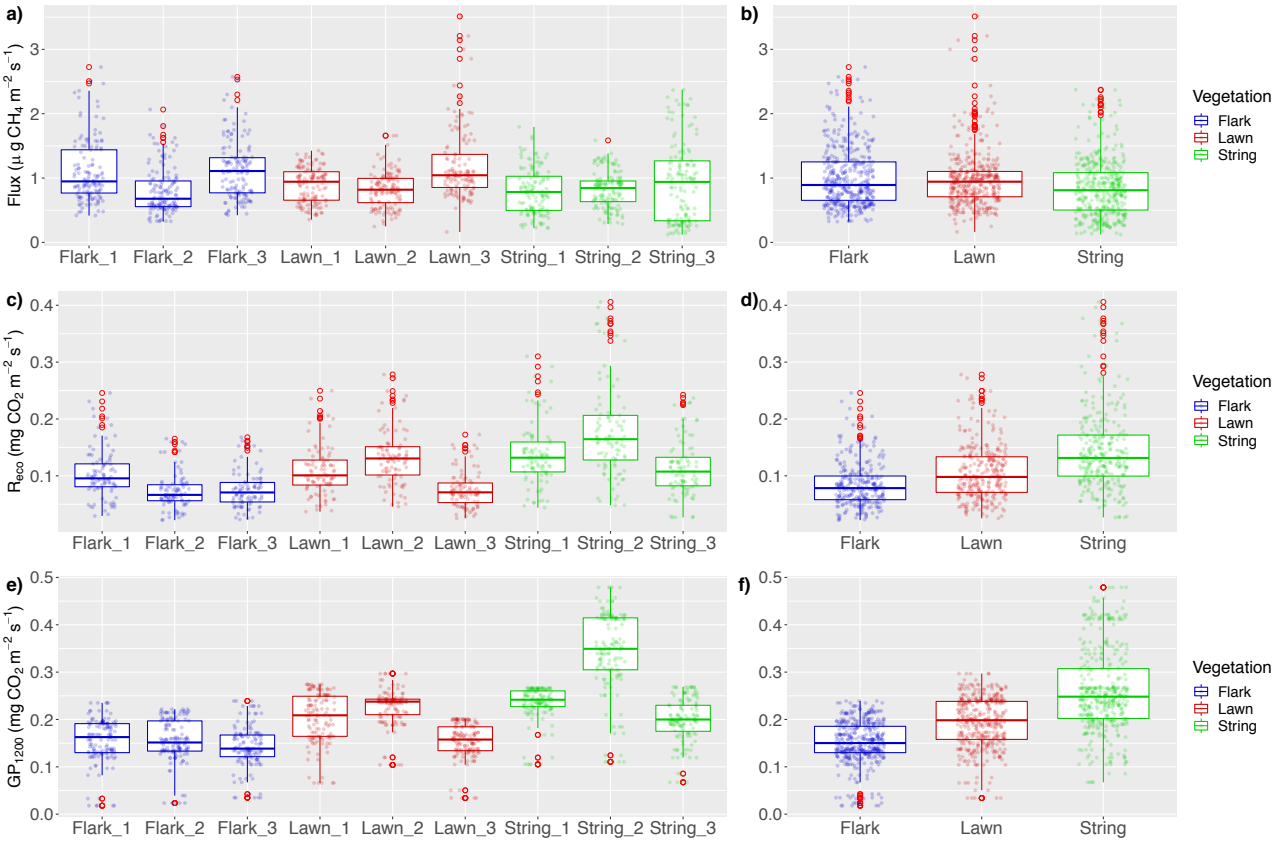

Figure 9. Differences in (a) CH_4 flux (c) respiration and (e) GPP_{1200} between measurement plots, as well as differences in (b) CH_4 flux (d) respiration and (f) GPP_{1200} between vegetation types.

3.5 Models

3.5.1 Variable selection

Overall correlations between variables were small (Fig. 10, and see appendix table 9 for r^2 values). Both chamber (r^2 = 0.76) and soil (r^2 = 0.88) temperature were highly correlated with air temperature. Interestingly, the correlation between chamber and soil temperatures was under the value of 0.7 (r^2 = 0.67). Therefore, both soil and chamber temperature could be used in the same models.

PAR was negatively correlated with relative humidity (r^2 = -0.76). Both of these variables describe weather conditions with high PAR indicating sunnier, warmer and dryer day and high relative humidity indicating cloudy and damp days. Since relative humidity had a higher correlation with CH_4 flux (r^2 = -0.37) than PAR (r^2 = 0.21), it was chosen to be used in modelling.

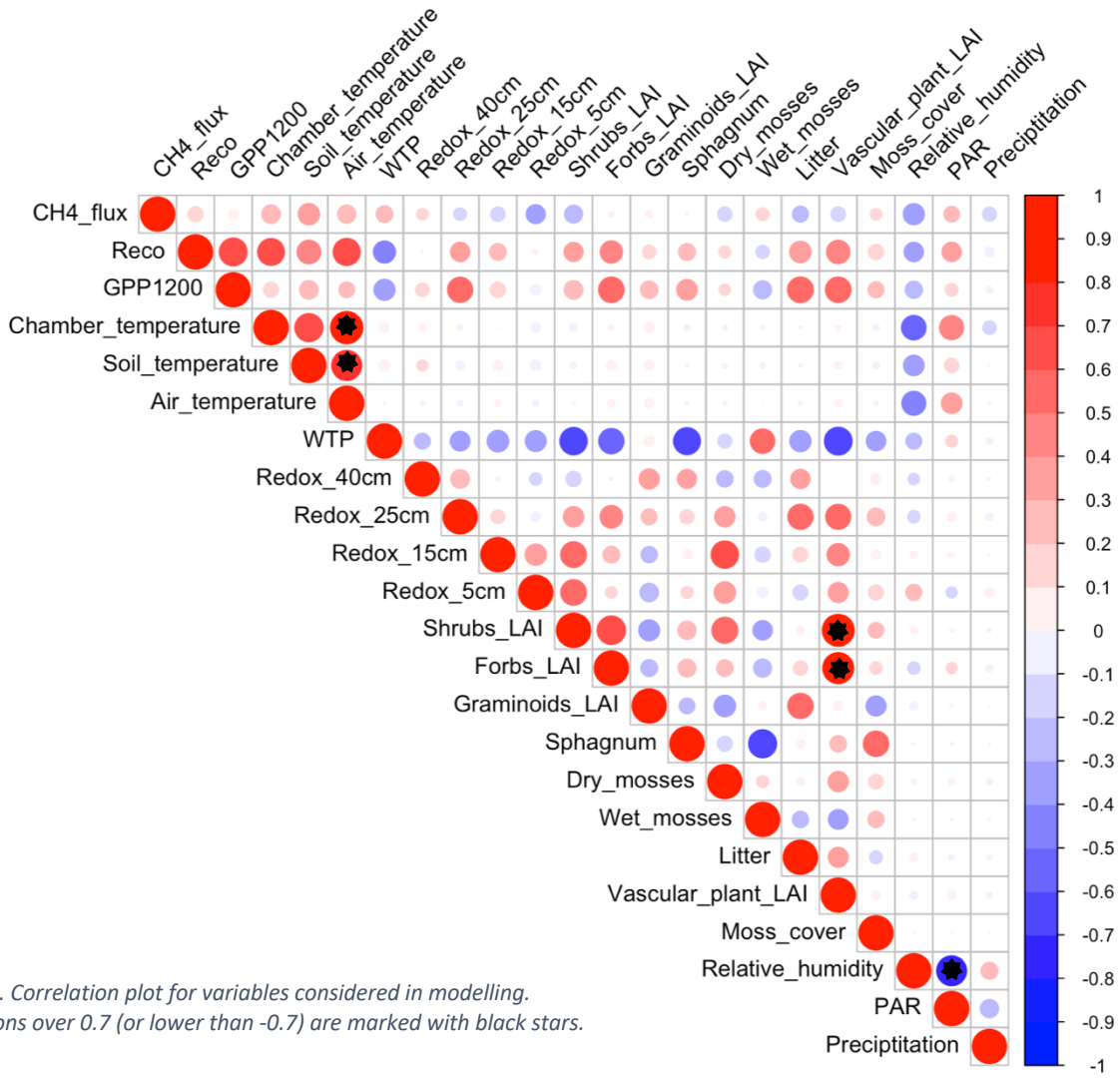

Figure 10. Correlation plot for variables considered in modelling. Correlations over 0.7 (or lower than -0.7) are marked with black stars.

Both shrub LAI (r^2 = -0.86) and forb LAI (r^2 = -0.81) correlated positively with vascular plant LAI which is expected since vascular plant LAI was calculated as the sum of both of these variables and graminoid LAI. For the model correlation between these variables is, however, not relevant since they would anyways not be included in the same model.

Correlation between R_{eco} and GPP_{1200} (r^2 = -0.66) was below the determined rejection level. R_{eco} was nevertheless dropped out of modelling since both R_{eco} and CH_4 flux are affected by processes occurring in peat and therefore are controlled by the same environmental variables. GPP_{1200}, on the other hand, reflect photosynthetic activity, which describes the processes that produce substrate for bacteria in the soil. It is thus more relevant to include GPP_{1200} in the model.

After omissions due to observed cross-correlations, variables chosen to be used in modelling were all redox and vegetation variables together with GPP_{1200}, WTP, soil and chamber temperature, relative humidity and precipitation.

3.5.2 GAM model

Model 3 was the best performing GAM (AIC 10.91), but AIC of Model 1 (AIC 13.32) was not much higher (Table 9, see appendix table 10 for results of all models). It, therefore, appears that including moss variable as separate functional groups does not improve the model. Furthermore, none of the individual moss function groups were statistically significant in Model 1 (See appendix table 10). Models 2 and 4 had considerably larger AIC values (AIC 49.03 for both models), which indicates that grouping vascular plants into one variable does not adequately capture the influence of the individual functional groups. Model 5 had clearly the largest AIC of 103.85. In this model vegetation community type was the only vegetation variable, and therefore, it appears that simple categorization of vegetation is not able to describe the influence of vegetation. Furthermore, vegetation type was not significant in Model 5 (Appendix table 10).

Table 9. AIC and R^2 values for the five initial models with different combinations of vegetation variables.

Model	AIC	R^2 adjusted
Model 1	13.32	0.718
Model 2	49.03	0.692
Model 3	10.91	0.724
Model 4	49.03	0.692
Model 5	103.85	0.640

The five initial models were able to explain 64,0 % to 72,4 % of the observed variation in CH_4 flux. Adjusted R^2 followed the pattern of AIC values with highest for Model 3 and lowest for Model 5 (Table 9). Model 5 that had vegetation type as the only vegetation variable explained 8.4 % less of the observed variation in CH_4 than the best model with functional groups and 5.2 % less than the worst model that included plant functional groups. This further strengthens the observation that at the studied fen categorizing vegetation into the three groups is not able to predict CH_4 flux.

Most variables in the bet GAM model were statistically significant (Table 10). From the significant variables all p-values were highly significant ($P < 0.001$) for all other variables except precipitation ($P = 0.038$). However, there was also a few other variables that were not significant. Redox potential at all other depths than 40 cm were not significant variables. Other nonsignificant variables were graminoid LAI ($P = 0.150$) and moss cover ($P = 0.061$). The random variable measurement plot was also significant in the model, indicating that the spatiality of plots influenced CH_4 flux.

Table 10. Edf and p-values for the best model (Model 3). P-values marked with colour as follows: read when P < 0.002 and green when 0.05 > P > 0.01.

Variable	edf	P-value
GPP_{1200}	1.828	0.000
Chamber T	1.461	0.000
Soil T	1.855	0.000
Relative humidity	1.111	0.000
Precipitation	0.776	0.038
WTP	1.923	0.001
Redox 40 cm	1.254	0.000
Redox 25 cm	1.532	0.078
Redox 15 cm	0.661	0.083
Redox 5 cm	0.738	0.051
Shrubs LAI	1.470	0.000
Forbs LAI	1.777	0.000
Graminoids LAI	1.646	0.150
Moss cover	0.703	0.061
Litter	1.874	0.000
Plot	6.789	0.000

The response of CH_4 flux to changes in the values of the variables was for most variables almost linear (Fig. 11). Nonetheless, several variables also show curved responses. Soil temperature had a rising curve, indicating that CH_4 flux was larger at higher temperatures. This is a response one would expect if methane-producing processes are more efficient at higher temperatures. However, the response of CH_4 flux to chamber temperate is not as intuitive. There is a rise in the curve at higher temperatures, but the curve also rises when moving toward lower temperatures. Therefore, high temperatures inside the chamber do as expected increase CH_4 flux, but CH_4 flux is also higher when the temperature is low. This effect might be due to that soil temperature more strongly affect CH_4 flux and interactions between the two temperatures might lead to the shape of the curve for chamber temperature.

WTP has the opposite form of the chamber temperature curve were the largest CH_4 flux occurred at an optimal water table of about 15 cm below the peat surface. Deviations from this WTP had lower CH_4 flux. Precipitation and relative humidity despite being significant in the mode had only a small influence on CH_4 flux, with both having what seem to be a negative somewhat leaner response. The curve for GPP_{1200} was rising at the beginning but flattened out towards the end. Increase in GPP_{1200}, therefore, appear to at low values increase CH_4 flux, but when GPP_{1200} reaches higher values increase in GPP_{1200} will no longer affect CH_4 flux. This effect can be accounted for

with spatial differences in GPP_{1200} between plots, but strong temporal variation in GP_{1200} through the growing season likely is more prominent and responsible for the shape of the curve.

The response of CH_4 flux was among the largest for vegetation variables forb and shrub LAI. Forb had a rising curve, whereas the effect of shrubs was the opposite and had a descending curve. Graminoid and mosses that were not statistically significant in the model had a much smaller effect. Redox potential from 5 and 15 cm also had a small effect on CH_4 flux, and the curves appear to be almost flat lines. CH_4 flux had, on the other hand, a considerable response to redox potential from 40 cm, which is about as large of an effect on CH_4 flux as shrubs and forbs have. Redox from 25 cm was the only redox variable with a rising curve. The response of CH_4 flux to redox at 25 cm is furthermore larger than for redox potential at 5 or 15 cm.

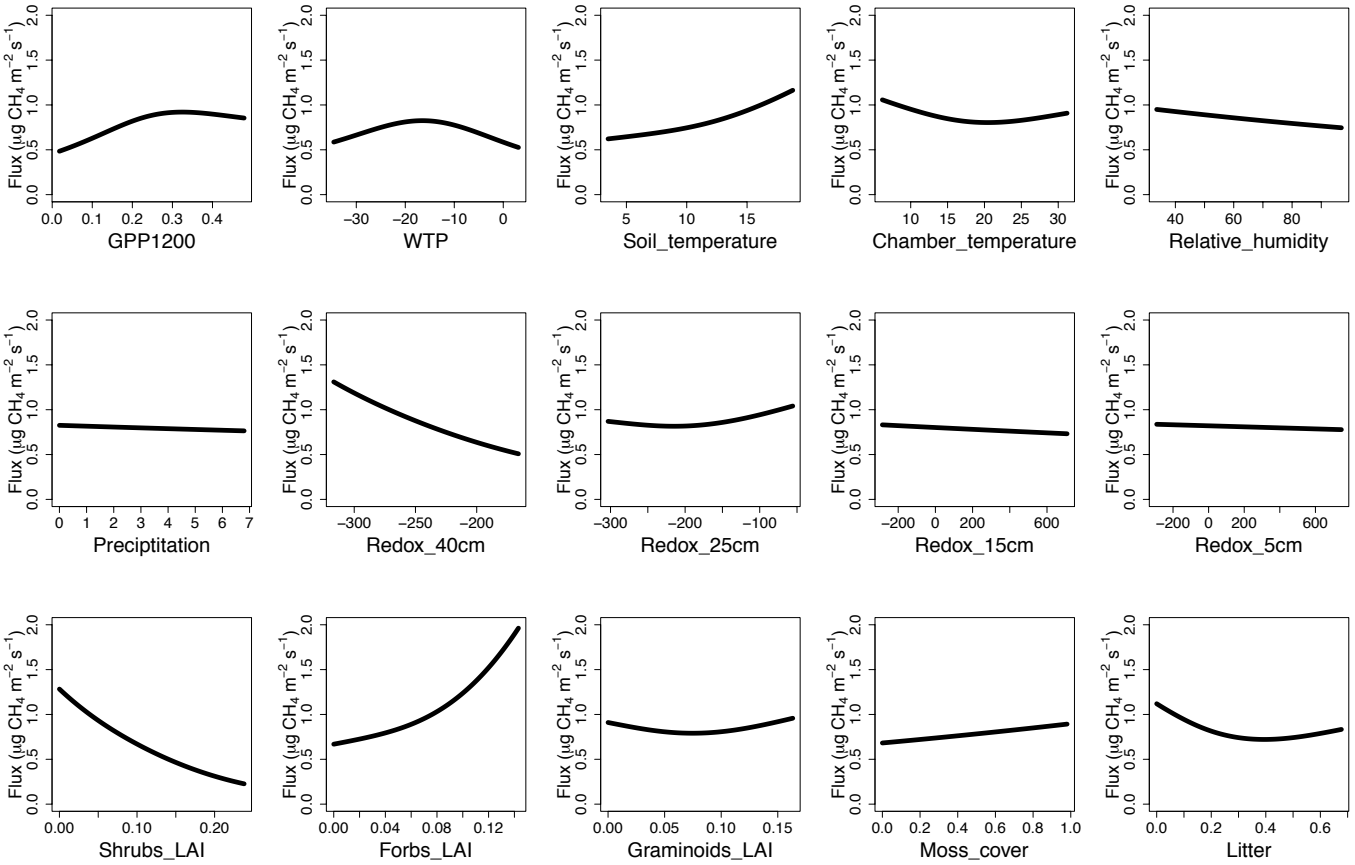

Figure 11. The curve of CH4 flux response to all variables included in the best model.

The interpretation from response curve of CH_4 flux to variables in the best model (Fig. 10), is reflected in the calculated values of loss of explanatory power when variables were removed from the model (Table 11). The largest decrease in explanation power of 7.8 % was seen when all vegetation variables were removed from the model. Closer inspection showed that especially

forbs had a large effect on the model's explanation power, but also shrubs and litter had a relatively large effect. Moss cove and graminoid LAI had a negligible effect on the explanation power, and in fact, removing these variables resulted in lower AIC than the full model has. GPP_{1200} also had a considerable effect on the model explanation power, which was though smaller than for shrubs, forb or litter.

Table 11. Edf and p-values for the best model (Model 3). AIC values that are lower than the AIC for the full model are highlighted with red.

Variable removed	AIC	R^2 (adj)	Change in r^2	%
None	10.91	0.704	0.000	0.0
Vegetation	96.03	0.627	-0.078	-7.8
Vascular plant LAI	74.12	0.648	-0.057	-5.7
Shrub LAI	32.19	0.683	-0.021	-2.1
Forb LAI	70.55	0.652	-0.052	-5.2
Graminoid LAI	7.97	0.701	-0.003	-0.3
Moss cover	6.37	0.703	-0.002	-0.2
Litter	26.83	0.687	-0.017	-1.7
Redox	33.16	0.681	-0.024	-2.4
Redox 40 cm	31.06	0.684	-0.020	-2.0
Redox 25 cm	9.00	0.700	-0.004	-0.4
Redox 15 cm	6.84	0.702	-0.002	-0.2
Redox 5 cm	6.48	0.702	-0.002	-0.2
GPP_{1200}	25.26	0.688	-0.016	-1.6
Temperatures	45.97	0.671	-0.033	-3.3
Soil temperature	29.81	0.685	-0.019	-1.9
Chamber temperature	14.78	0.696	-0.009	-0.9
WTD	27.76	0.686	-0.018	-1.8
Relative humidity	15.72	0.696	-0.009	-0.9
Precipitation	6.77	0.702	-0.002	-0.2

Removing both temperatures decreased the explanation power by 3.3 %, which is a considerable effect, but still not close to the effect of vegetation variables. Furthermore, the effect of forbs alone exceeded the effect of removing temperatures had on the model. Soil temperature seems to be more important since when it was removed, it had an impact on the model explanatory power close to the effect of shrubs. Chamber temperature had a much smaller effect but removing this variable still increase the AIC. WTP was about as important to the model as soil temperature. Relative humidity, on the other hand, had the same effect as chamber temperature.

Perception, even thou it was significant in the model, had only a minimal effect on the explanation power. Furthermore, removing this variable improved the AIC value.

When all redox variables were removed r^2 of the model decreased with 2,4 %. Redox at 40 cm, was, however, the only redox variable with a considerable effect on the explanatory power. Removing any of the other redox variable beardly reduced the explanatory power, even though redox from 25 cm had a slightly larger effect on the model explanatory power (0.4 %) than redox potential from 5 or 15 cm (0.2 %). Nevertheless, when redox from 5, 15 or 25 cm was removed the AIC of the model decreases from the AIC value of the full mode, indicating that none of these variables was important to the model.

3.6 Temporal autocorrelation

Temporal autocorrelation of residuals of the best model (Model 3) was relatively small (Appendix fig. 3). Autocorrelation for a lag of one day was on average around 0.4, but for a lag of two days autocorrelation was for most measurement plots already greatly reduced (average around 0.2). For some plot autocorrelation increased again with a lag of 3-5 days, however, no plot showed considerable negative autocorrelation at longer lags of around 15 days. String_3 differed from other plots in having a bit higher positive autocorrelation at a small lag, but this plot did not either show negative autocorrelation at longer lags. Furthermore, residual for the model were normally distributed (Appendix fig. 2 c) and no obvious pattern was present in the residual plot (Appendix fig. 2 b). Overall, these results show that predictions of the model should be reliable.

4. Discussion

4.1 Spatial variability of CH_4 fluxes

Overall variation in CH_4 flux was considerable and varied from almost zero(0.12 μg CH_4 m^{-2} s^{-1}) to 3.51 μg CH_4 m^{-2} s^{-1}. All the observed fluxes were above zero, indicating that Halssiaapa was a source of CH_4 during the whole study period. Dinsmore et al. (2017) conducted several chamber measurements at Halssiaapa during the growing season of 2012 and also found that wetland plots were sources of CH_4. Mean flux (1.56 ± 0.20 mg C m^{-2} h^{-1} ≈ 0.59 ± 0.07 μg CH_4 m^{-2} s^{-1}) measured by Dinsmore et al. (2017) was somewhat smaller than the mean flux of this study in 2019 (0.94 ± 0.01 μg CH_4 m^{-2} s^{-1}). Dinsmore et al. (2017), however, performed their measurements much later into the growing season and as seen in the data of this study (Fig. 8 a) fluxes are generally lower towards the end of the growing season. Therefore, the mean flux observed by Dinsmore et al. (2017) can be expected to be lower.

CH_4 fluxes differed between the vegetation types with strings having lower CH_4 flux than flarks and lawns. Similar results were found from Canadian mires by Bubier (1995) where dryer hummocks had low CH_4 flux. Bubier (1995), however, also found that lawns had higher CH_4 flux than hollows, but that was not seen at Halssiaapa. When exploring differences between plots inside certain vegetation types, plots Lawn_3 and Flark_2 differed from other plots in their vegetation type (Fig. 8 a). Lawn_3 had higher CH_4 flux than other lawn plots and was actually more similar to the flark plots. This plot was mostly dominated by *Sphagnum* mosses and had not similar vegetation characteristic as the other two lawn plots (Fig. 7). Such *Sphagnum* dominated lawns may, therefore, have higher CH_4 fluxes than other lawns. However, Lawn_3 was the only such plot in this study which makes it hard to make any strong conclusions and more measurements would be needed to distinguish if CH_4 flux from *Sphagnum* lawns indeed does differ from the other lawn surfaces. Plot Flark_2 differed from flark plots in hawing lower CH_4 flux that was more similar to Lawn_1 and Lawn_2. Vegetation at this plot differed from all other plots in the sense that it was almost totally covered by dead organic matter and had less living vegetation, especially vascular plants. This may indicate the importance of living vegetation to CH_4 flux, especially at wetter plots.

Classification of measurement plots into three vegetation types did cluster plots into groups with distinctly different WTP and vegetation characteristics. Despite this, vegetation type was able to explain only 2 % of the observed variation in the CH_4 fluxes. Individual measurement plots were,

however, not either able to explain much more of the observed variation (11 %). Even though CH_4 fluxes differed between both vegetation types and plots, variation within groups was large and range of fluxes for all measurement plots overlapped with each other (Fig. 9 a and b). This suggests that small-scale spatial variability in CH_4 flux within the mire is small and is dominated by the temporal variation. Minkkinen and Laine (2006) found similar results from Finnish mires where differences in CH_4 flux between vegetation types were small at nutrient-rich fens. However, there might be more pronounced differences at a larger-scale between different areas of the mire. Actually, Dinsmore et al. (2017) who had their measurement plots at several locations around the mire found relatively large differences between their measurement plots.

4.2 Controls of spatiotemporal variation in CH_4 fluxes

The best model was able to explain 72 % of the observed variation in CH_4 flux, which is on the higher end of the reported values. For example, in modelling CH_4 flux across several mire sites Turetsky et al. (2014) were able to explain 65 % and Christensen et al. (2003) almost the 100% the of variation in CH_4 flux. Granberg et al. (1997) were able to explain 36 - 75 % of the variation in CH_4 flux for individual mire sites. These studies, however, had fewer explanatory variables in their models, but on the other hand, many of the models included interaction terms between variables, which were not included in the models of this study. Overall, several variables were important in models, which points to that CH_4 flux depends on various processes that are affected by several factors.

4.2.1 Temperature

Both soil and chamber temperature were important variables in the best model, with soil temperature having the greatest effect on the model explanatory power. This is consistent with previous studies that identify soil temperature as a key factor affecting the CH_4 flux (e.g. Lloyd et al. 1998, Dinsmore et al. 2017). Furthermore, the form of the relationship between soil temperature and CH_4 flux where CH_4 increased with increasing temperature, is in line with previous results from laboratory experiments (Dunfield et al. 1993, Bergman et al. 1998, Lloyd et al. 1998) and field studies (Granberg et al. 1997, Christensen et al. 2003, Dinsmore et al. 2017). The temperature within the chamber had a smaller effect on the model's explanatory power. Furthermore, the shape of the CH_4 flux response to chamber temperature does not follow the same form as for soil temperature. In fact, according to the model, CH_4 flux is higher at lower

temperatures (Fig. 11). It may be that soil temperature already explains most of the effect temperatures have on the CH_4 flux. This was supported by that soil temperature was more important in the model than chamber temperature. Air temperature changes faster than soil temperature, and therefore, even though the temperature inside the chamber is low soil temperature may remain relatively high. This could lead to that methanogens are active in the warm soil when air temperature is low, which could explain the bell-shaped response of chamber temperature. Furthermore, a simple linear correlation between chamber temperature and CH_4 flux was positive ($r^2 = 0.30$), suggesting that CH_4 flux was nevertheless larger at higher temperatures.

4.2.2 Water table position

WTP was about as important to the model as soil temperature. In previous studies both negative (eg. Dinsmore et al. 2017) and positive (e.g. Granberg et al. 1997, Strack et al. 2014) relationships between CH_4 and WTP have been observed. The response curve of WTP was bell-shaped (Fig. 10), with largest CH_4 flux at an optimal WTP of about 15 cm. This makes both positive and negative relationships to WTP possible, where if WTP drops below the optimal WTP CH_4 flux decreases creating a positive correlation. CH_4 flux also decreases when WTP rises above the optima level which results in a negative relationship. A similar response was found by Turetsky et al. (2014) in comparisons between 71 different wetlands, where poor fens had an optimal WTP located slightly below the peat surface and rich fen an optimal WTP above the peat surface. This is higher than the optimal WTP, which is about 15 cm below the peat surface, identified at Halssiaapa.

4.2.3 Relative humidity and precipitation

Relative humidity and precipitation were both significant variables in the best model, but despite this, their effect on CH_4 flux was insignificant when compared to the other variables. RH and precipitation likely do not directly influence CH_4 flux, but rather indicate conditions of other factors that can affect CH_4 flux. Low RH could, for example, indicate sunnier days with higher temperature and primary production. Precipitation, on the other hand, affects WTP. Precipitation was recorded as daily values which probably only reflects temporary changes in WTP. Average precipitation for longer periods, like weeks, could possibly have been a better indication of the long-term effect on WTP. Indeed, mean annual precipitation was found to be a significant predictor of CH_4 flux by Turetsky et al. (2014).

4.2.4 Vegetation properties

Vegetation properties had a considerable effect on CH_4 flux, as removing them reduced the model's explanatory power considerably. Vegetation properties grouped together had actually a greater effect on the model's explanatory power than temperature and WTP combined. This would support the suggestion of Turetsky et al. (2014) that at fens the influence of vegetation could potentially override the effect of temperature and WTP. Despite the effect of individual vegetation properties, categorization into three main vegetation types was not able to describe the effect of vegetation, as the model with only vegetation categories performed worse than any mode including plant functional groups.

Forb LAI was the most important plant variable in the best model, where CH_4 increased toward higher forb LAI values. Bubier (1995) fount that *Menyanthes trifoliata* was a good indicator of wet surfaces with high CH_4 flux. This species was one of the most common forbs found at the study site and therefore forb LAI could indicate wet surfaces with a higher CH_4 flux. However, it can be questioned how much spatial variation can be explained by this variable since the model included a random variable that possibly explains most of the spatial variation instead of the fixed variables in the model. An explanation that considers temporal changes in forb LAI could thus more likely be behind the observed pattern. One such explanation is the transport of CH_4 through vascular plants to the atmosphere and forbs could in this way directly influence CH_4 flux. Indeed, Öquist & Svensson (2002) found that CH_4 transportation was especially important in fens with larger plant biomass than bogs. As forb LAI changes through the growing season as do the amount of CH_4 that can travel through these plants, which can explain temporal variation in CH_4 flux.

Graminoids could also be important in CH_4 transportation and, for example, Turetsky et al. (2014) and Bellisario et al. (1999) found that greatest CH_4 fluxes occurred at sites where graminoid were the dominant vascular plant. However, graminoids had here no effect on modelled CH_4 flux and it was not significant in any of the five models (Appendix table 8). This could be due to that overall graminoid cover was low at the study site and graminoid abundance varied much less than the abundance of forb during the growing season.

Shrub LAI was the second most important vegetation variable after forb LAI. The influence of shrubs LAI on CH_4 flux is opposite to the effect of forbs, where CH_4 flux is highest when shrub LAI is

low. Therefore, it appears that shrubs do not considerably contribute to CH_4 transportation. Shrubs preferred drier habitats and mostly occurred on stings plots. Similar results have been reported in many studies (Bubier 1995, Nilsson et al. 2001, Turetsky et al. 2014), where shrubs indicated lower WTP and CH_4 flux. However, this does not explain temporal variation, but instead spatial variation, and therefore, it can again be questioned if the influence on spatial variation is enough to account for the importance of shrubs in modelling CH_4 flux. Another explanation could be that plants can facilitate the transport of oxygen to anaerobic peat (Lloyd et al. 1998), which creates a zone of methane oxidation around plant roots. If shrubs are more effective at transporting oxygen into peat than at transporting CH_4 to the atmosphere the direct influence of shrub to CH_4 flux would be negative. Then again, shrubs occurred at drier places where the aerobic layer is anyways thicker, and thus, transportation of oxygen could be seen to have a minor effect on CH_4 oxidation. The observed negative relationship may, therefore, be more likely contributed to that shrub indicate spatial differences in WTP, and possibly to minor extent transportation of oxygen.

Bryophytes are sensitive to WTP fluctuations, and Bubier (1995) showed that bryophytes are a good indicator of long-term WTP, and therefore, also of CH_4 flux. Moss cover was, however, not significant in the best model and it had only a small effect on the explanation power of the model when removed. Bryophytes are a broad group including all mosses and therefore some species in the group prefer dyer habitat and other wetter habitat. This confounds the ability of the group as a whole to predict CH_4 flux. Nevertheless, even a finer grouping to sphagnum, wet and dry mosses was not either able to predict CH_4 flux. Similarly, Turetsky et al. (2014) found no significant effect of no vascular plant function groups on CH_4 flux but did identify vascular plant functional groups as important. This result points to that than even though bryophyte might be better indicators of WTP, vascular plants can better explain CH_4 flux. This could be due to the ability of vascular plants to directly affect CH_4 flux through transportation of CH_4. However, Strack et al. (2014), who also found that vascular plants were an important controller of CH_4 flux suggested that this because vascular plants are more easily degradable and therefore can provide a better substrate for microorganism than mosses. The direct effect of vegetation is hence not only through CH_4 transportation but also through the input of substrate for the microorganism in peat.

The input of substrate can further explain the positive influence of easily degradable forbs on CH_4 flux and why shrubs that have lower primary production as well as slowly degrading woody parts do not have such a positive effect on CH_4 flux. In addition, the effect of primary production can be seen in the importance of the GPP_{1200} variable. The response curve describes a relationship, where primary production increases together with CH_4 flux, but at as $GPPP_{1200}$ increases the effect levels out until input of more substrata no longer increase CH_4 flux. Such a curve can be seen when at in the beginning input of substrata stimulate CH_4 production, but at some point, substrata are no longer limiting and will stop to have an effect on CH_4 flux. Öquist & Svensson 2002 show similar results were CH_4 flux from fen was less dependent on primary production than CH_4 flux from bogs.

The response of CH_4 to litter could also strengthen the conclusion that transportation of CH_4 is more important than substrata provision of vascular plants. If substrate provision is more important, one could imagine that when there is a lot of dead organic matter CH_4 would be higher. This is, however, not the case and instead CH_4, flux was smaller when there was more litter. This could be due to that when there is a lot of litter there are fewer living plants that can function as CH_4 transport pathways. Furthermore, living plants also contribute to substrata provision through root exudates, and therefore, could be enough to provide substrata for microorganism at fens where substrate is not that limiting in the first place.

4.2.5 Redox potential

Redox potential measures from all depth had at least a small effect on the model explanation power when removed, but redox form 40 cm was the only redox variable with a significant effect on CH_4 flux. However, it could be expected that redox potential closer to the surface would better be able to explain CH_4 flux since WTP was high at the study site, and therefore, fluctuations in WTP would be expected to affect redox at the shallower depths. Indeed, fluctuation in redox potential for the shallower depths (5 cm and 15 cm for String_1) were larger than for redox potential from the deeper measurement depths (25 and 40 cm) (Fig. 6).

For most lawn and string plots redox potential increased towards the end of the measurement period, which coincided with a decrease in WTP thought the whole study site. This could reflect a connection between redox potential and WTP. Redox potential of 700 to 400 mV is generally considered to occur when oxygen is present in soil (Wang et al. 1993, Yu et al. 2001). Since redox

potential at the surface reached values of around 500 to 700 mV at the latter half of the measurement period it can be assumed that oxygen was present in this peat layer. Therefore, the decrease in WTP seems to have created an aerobic layer at the peat surface. A negative relationship between WTP and redox potential at mires from Poland and Netherlands was reported by de Mars & Wassen (1999), which supports the conclusion that redox potential is higher when WTP is lower. The response of redox potential did, however, not always reflect the WTP. For example, String_2 had the lows WTP despite that redox potential at all depth remained low (under -100 mV) at this plot under the whole measurement period. Furthermore, in flarks redox potential at 5 cm fluctuated considerably and occasionally reached high redox potential values at the beginning of the measurement period, even thou at this time WTP at the plot was either over or just under the peat surface. When WTP is over the peat surface oxygen could be mixed into the open water surface and in this way, oxygen might occasionally be present in the upper peat layer even though it is flooded. This might explain why according to redox potential oxygen was sometimes present in the upper peat layer of flarks when WTP was high.

Despite the connection to WTP fluctuation and more importantly presence of oxygen, redox potential close to the surface was not a significant predictor of CH_4 flux. This might indicate that the oxidation of methane is not as strong of a determiner of methane flux as the rate of methane production. Isotope analyses performed by Bellisario et al. (1999) show that oxidation was, indeed, of smaller importance at Canadian mires than CH_4 production. Furthermore, even when there is oxygen present in the uppermost peat layer, several anaerobic microenvironments may persist. Indeed, Knorr et al. (2009) found that redox potential was only partly connected to WTP at a fen with dens peat where anaerobic microenvironments could be thought to persist even when WTP is low.

Redox potential deeper down on the peat in contrast to redox further up, remained more stable and did not present such sudden changes, as for redox potential near the peat surface did. Since redox from 40 cm was the only significant redox variable in the models, redox potential at this depth might reflect more long-term changes in peat chemistry than redox further up that is more easily affected by short-term changes in for example WTP. Redox potential at 40 cm was always below the water table level and redox at 25 cm was most of the time under the WTP. This is also reflected in redox potential that was the lowest for these two depths and never reached over 0

mV. Redox potential thus points to that these parts of the peat layer are anaerobic, and oxygen is not present. Therefore, the presence of oxygen should not limit CH_4 production, but alternative electron acceptors might still be used. In laboratory studies, methanogenesis has been identified to start at about -150 to -201 mV (Wang et al. 1993, Yu et al. 2001), but methanogenesis has likewise been reported to occur at higher redox potentials (between +50 to 0 mV) (Peters & Conrad 1995). Redox potential at 40 cm had a max value of -163.7 mV and it is thus constantly below initiation level of CH_4 production and CH_4 is likely constantly produced at this depth.

Despite similarities in redox potential between depth of 25 and 40 cm, CH_4 flux has a different response to redox potential at a depth of 25 cm than other depths. In fact, it seems that CH_4 production increases when redox potential increases, which is the opposite of the negative relationship between CH_4 flux and redox potential from all other depths. Wang et al. (1993) and Yu et al. (2001) also recorded a negative exponential relationship between CH_4 flux and redox potential. However, a positive relationship was reported by Yao et al. (1999), but this was for comparisons of several different soil type and when individual soils were considered separately a negative relationship was present. Nonetheless, redox potential from 25 cm was not significant in the model and its effect on CH_4 flux was small. These previous studies have been performed in controlled laboratory condition and the relationship between CH_4 flux and redox potential has not been well studied in filed conditions. A negative connection between CH_4 flux and redox potential that has been observed in laboratory conditions, for the most part, holds up in this field study.

Another explanation for why redox deeper down is the only significant redox variable is how CH_4 is produced in different peat layers. In the uppermost parts of the anaerobic layer, CH_4 is mostly produced through acetate fermentation (Hornibrook et al. 1997). Since acetate fermentation does not rely on reduction processes it is reasonable to assume that it would not be as severely affected by the presence of alternative electron acceptors as the production of methane through CO_2 reduction. Therefore, methane production at the shallower depts may not be as sensitive to changing redox potential. Still, the presence of oxygen does disrupt this process since methanogens do not tolerate oxygen, and thus some level of response to redox potential could still be expected. However, the impact of CH_4 oxidation on total CH_4 flux may be reduced by the transportation of CH_4 through plants that enable CH_4 produced in the deeper peat layer to bypass the oxidized surface layer. Redox potential at the deeper depth could than again be expected to

affect CH_4 production since in CH_4 deeper down is mostly produced through the reduction of CO_2. Keller & Bridgham (2007) found that CO_2 reduction constitutes only a small part of the total methane production at fens that have higher primary production than bogs and therefore produce more CH_4 through acetate fermentation. Since redox potential at the deepest measurement depth had an effect at this studied fen these measurements could be an even better indicator of CH_4 flux at bogs.

4.3 Evaluation of methods

When it comes to considering the effect of CH_4 transportation through plants the CH_4 flux measurement method has to be taken to account. It can be argued that opaque chamber measurements are not ide to capture this effect since it has been shown that CH_4 transportation is largest when plants are photosynthetically active (Joabsson et al 1999, Whalen 2005). Thus, this effect of photosynthesis on CH_4 transportation might not be captured in the absence of light. Despite this, Öquist and Svensson (2002) found an effect of shoot number on CH_4 flux from opaque chamber measurement, which points to that CH_4 transportation through plants in the absence of light nonetheless has a noticeable influence on CH_4 flux. Furthermore, when comparing CH_4 flux from transparent and opaque chamber measurement performed in this study, there was no significant difference in mean flux from the two types of chambers. The influence of using mostly opaque chamber measurements should thus be minimal.

Considering the models, one has to remember that results are always to some extent dependent on how models were constructed, in other words, which structure and variable were included in models. This explains why the five initial models with different combinations of vegetation variables produced slightly different results (Appendix table 10). For instance, which redox potentials that were identified as significant differed between the models. In the best model redox potential from 40 cm was the only significant redox variable, whereas, in some of the other models, redox potentials from also 25 and 5 cm were significant. Furthermore, cross-correlations between variables may also influence the response curves of variables, as may be the case for chamber temperature discussed earlier. Temporal autocorrelation is also a factor that can affect the result. Nevertheless, temporal autocorrelation was relatively small and there was no obvious influence on residuals of the best model. Thus, despite some uncertainties in the result given by modelling the overall picture is the same for all models.

5. Conclusions

Chamber measurements were conducted at a boreal fen in northern Finland during the growing season of 2019 in order to explore small-scale spatial and temporal variation in CH_4 flux and to identify controllers behind observed variation. Spatial variation at the studied fen was present but small and temporal variation through the growing season appeared to dominate the variation.

Temperature and water table position which have been identified in many earlier studies to control the CH_4 fluxes (e.g. Turetsky et al. 2014) were also here among the most important factors influencing CH_4 flux in this study. Vegetation properties were, however, the most important factor affecting the CH_4 flux. Especially vascular plants were found to have a greater effect on the CH_4 flux than temperature or water table position. Vegetation can indicate spatial variation in WTP that is connected to variation in CH_4 flux but also affect CH_4 flux directly by transportation of CH_4 through plant tissues and by providing substrate for microorganisms through primary production. Substrate availability played an important role in controlling CH_4 production, but it seemed to limit the production of CH_4 only when primary production was low. Transportation of CH_4 through plants, on the other hand, may have had a stronger influence on CH_4 flux. Even though vegetation properties had a clear influence of on CH_4 flux, categorization into three vegetation types could not capture the impact of vegetation. Instead, information about plant functional groups was needed. This information could potentially be used when predicting CH_4 flux over larger areas by using remote sensing to map vegetation characteristics that can then be used to estimate CH_4 flux.

Redox potential in lower peat layers was found to be an important variable in the CH_4 flux model. Redox potential is relatively easy to measure, and results suggest that it could provide a useful tool to aid in improving spatiotemporal extrapolation of CH_4 fluxes. Redox potential closer to the surface was not found to be a significant factor in the best model. This could indicate that oxidation of CH_4 is not as important in controlling CH_4 flux as the production of CH_4, or that CH_4 production near the surface that mostly takes place through acetate fermentation is not as severely affected by redox conditions as CO_2 reduction that is the dominant CH_4 production pathway in deeper peat layers. Redox potential could thus be a particularly good indicator of CH_4 flux in areas where methane is produced primarily through CO_2 reduction, like bogs. The observed conditions, however, apply only to the studied area and more field studies on the relationships to redox potential are needed to be able to generalize results to larger areas.

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Appendix

Table 1. Dates of chamber measurements and which measurement chamber where used.

Date	Measurements
26.6.2019	Both dark and light chambers
27.6.2019	Only dark chambers
30.6.2019	Both dark and light chambers
1.7.2019	Only dark chambers
2.7.2019	Only dark chambers
4.7.2019	Only dark chambers
5.7.2019	Only dark chambers
8.7.2019	Both dark and light chambers
9.7.2019	Only dark chambers
10.7.2019	Only dark chambers
11.7.2019	Only dark chambers
12.7.2019	Both dark and light chambers
15.7.2019	Only dark chambers
17.7.2019	Only dark chambers
18.7.2019	Only dark chambers
19.7.2019	Both dark and light chambers
22.7.2019	Both dark and light chambers
23.7.2019	Both dark and light chambers
24.7.2019	Both dark and light chambers
25.7.2019	Only dark chambers
26.7.2019	Only dark chambers
29.7.2019	Only dark chambers
30.7.2019	Only dark chambers
31.7.2019	Both dark and light chambers
1.8.2019	Only dark chambers
2.8.2019	Only dark chambers
4.8.2019	Both dark and light chambers
5.8.2019	Only dark chambers
6.8.2019	Only dark chambers
12.8.2019	Only dark chambers
14.8.2019	Both dark and light chambers
15.8.2019	Only dark chambers
16.8.2019	Only dark chambers
19.8.2019	Only dark chambers
20.8.2019	Both dark and light chambers
21.8.2019	Only dark chambers
22.8.2019	Only dark chambers
24.8.2019	Both dark and light chambers
26.8.2019	Only dark chambers
27.8.2019	Only dark chambers
28.8.2019	Both dark and light chambers
30.8.2019	Only dark chambers
2.9.2019	Only dark chambers
3.9.2019	Only dark chambers
6.9.2019	Only dark chambers
16.9.2019	Only dark chambers
19.9.2019	Both dark and light chambers
20.9.2019	Only dark chambers
22.9.2019	Only dark chambers
23.9.2019	Only dark chambers

Table 2. List of vegetation survey dates.

Dates
30.5.2019
13.6.2019
27.6.2019
15.7.2019
26.07.2019
8.8.2019
22.8.2019
5-6.9.2019
18.09.2019

Table 3. List of species classified to the different functional groups

Shrubs	**Forbs**	**Graminoids**	***Sphagnum*-mosses**	**Dry mosses**	**Wet mosses**
Andromeda polifolia	*Melampyrum patense*	*Eriophrum russeolum*	*Sphagnum angustifolium*	*Aulacomnium palustre*	*Sarmentypnum* sp.
Vaccinium oxycoccus	*Comarum palustre*	*Carex magellanica*	*Sphagnum lindbergii*	*Liverwort* sp.	
Betula nana	*Menyanthes trifoliata*	*Carex canescens*	*Sphagnum riparium*	*Scapania* sp.	
	Scheuchzeria palustris	*Eriophorum vaginatum*		*Straminergon stramineum*	
	Drosera rotundifolia	*Carex limosa*			
		Eriophorum sp.			


String_1


String_2


String_3


Lawn_1


Lawn_2


Lawn_3

Figure 1. Overview of measurement plots. Pictures were taken on 17.7.2019

Table 4. Lis of variables included in modelling. Explanation of variable in the first column, shortening of the variable name in the second column, the type/group of the variable in the third column and unit of the variable in the fourth column.

Variable	Short	Type	Unit
Methane flux	CH_4 flux	Response	$\mu g\ CH_4\ m^{-2}\ s^{-1}$
Respiration	R_{eco}	Environment	$mg\ CO_2\ m^{-2}\ s^{-1}$
CO2 bound at 1200 PPFD	GPP_{1200}	Environment	$mg\ CO_2\ m^{-2}\ s^{-1}$
Soil temperature	Soil_T	Environment	˚C
Chamber temperature	Chamber_T	Environment	˚C
Air temperature	Air_T	Environment	˚C
Water table position	WTP	Environment	cm
Relative humidity	RH	Environment	%
Photosynthetically active radiation	PAR	Environment	$\mu mol/m^2s$
Precipitation	Precipitation	Environment	mm
Redox potential at 40 cm	Redox at 40 cm	Redox	mV
Redox potential at 25 cm	Redox at 25 cm	Redox	mV
Redox potential at 15 cm	Redox at 15 cm	Redox	mV
Redox potential at 5 cm	Redox at 5 cm	Redox	mV
Shrubs leaf area index	Shrubs LAI	Vegetation	LAI
Forbs leaf area index	Forbs LAI	Vegetation	LAI
Graminoids leaf area index	Graminoids LAI	Vegetation	LAI
Sphagnum cover	Sphagnum	Vegetation	%
Wet mosses cover	Wet mosses	Vegetation	%
Dry mosses cover	Dry mosses	Vegetation	%
Litter cover	Litter	Vegetation	%
Total vascular plant leaf area index	Vascular plant LAI	Vegetation	LAI
Total moss cover	Moss cover	Vegetation	%
Vegetation classified in three types	Vegetation type	Vegetation	Flark, lawn or string
Measurement plot	Plot	Random variable	9 plots

Table 5. Maximum, minimum and average WTP for all plots, vegetation types and the study area as a whole. Averages are given with standard error.

Plot	Maximum	Minimum	Avgrage
Flark_1	1.4	-10.0	-5.1 ± 0.32
Flark_2	3.1	-8.8	-3.7 ± 0.34
Flark_3	3.0	-12.4	-6.1 ± 0.45
Lawn_1	-4.3	-16.1	-11.1 ± 0.33
Lawn_2	-4.6	-16.6	-11.5 ± 0.34
Lawn_3	-7.3	-18.2	-13.3 ± 0.31
String_1	-15.3	-27.1	-21.9 ± 0.33
String_2	-35.5	-16.6	-28.0 ± 0.46
String_3	-32.0	-16.1	-24.9 ± 0.45
Flark	3.1	-12.4	-5.0 ± 0.22
Lawn	-4.3	-18.2	-12.0 ± 0.20
String	-35.5	-15.3	-25.0 ± 0.27
All	-35.5	3.10	-13.9 ± 0.27

Table 6. ANOVA test results with vegetation type and plot as a grouping factor.

Depth	Grupp	R^2	F	P
CH_4	Vegetation	0.023	14.29	7.35e-07
CO_2	Vegetation	0.028	88.75	<2e-16
GPP_{1200}	Vegetation	0.325	290.4	<2e-16
WTP	Vegetation	0.753	1924	<2e-16
Redox 40 cm	Vegetation	0.143	104.2	<2e-16
Redox 25 cm	Vegetation	0.283	246	<2e-16
Redox 15 cm	Vegetation	0.261	219.6	<2e-16
Redox 5 cm	Vegetation	0.143	104	<2e-16
CH_4	Plot	0.115	19.70	<2e-16
CO_2	Plot	0.317	48.14	<2e-16
GPP_{1200}	Plot	0.586	212.6	<2e-16
WTP	Plot	0.783	566.1	<2e-16
Redox 40 cm	Plot	0.862	967.7	<2e-16
Redox 25 cm	Plot	0.635	269.6	<2e-16
Redox 15 cm	Plot	0.803	632.3	<2e-16
Redox 5 cm	Plot	0.375	92.75	<2e-16

Table 7. Tukey HD tables for ANOVA test results with vegetation type and plot as a grouping factor for CH_4, CO_2 and GPP_{1200}. P values under the significance limit of 0.05 are marked with red.

Comparison	CH_4	CO_2	GP_{1200}
Flark-String	0.000	0.000	0.000
Lawn-String	0.000	0.000	0.000
Lawn-Flark	0.610	0.000	0.000
Flark_2-Flark_1	0.000	0.001	1.000
Flark_3-Flark_1	1.000	0.004	0.483
Lawn_1-Flark_1	0.002	0.994	0.000
Lawn_2-Flark_1	0.000	0.002	0.000
Lawn_3-Flark_1	0.396	0.003	1.000
String_1-Flark_1	0.000	0.000	0.000
String_2-Flark_1	0.000	0.000	0.000
String_3-Flark_1	0.039	0.858	0.000
Flark_3-Flark_2	0.000	1.000	0.505
Lawn_1-Flark_2	0.661	0.000	0.000
Lawn_2-Flark_2	1.000	0.000	0.000
Lawn_3-Flark_2	0.000	1.000	1.000
String_1-Flark_2	1.000	0.000	0.000
String_2-Flark_2	1.000	0.000	0.000
String_3-Flark_2	0.162	0.000	0.000
Lawn_1-Flark_3	0.000	0.000	0.000
Lawn_2-Flark_3	0.000	0.000	0.000
Lawn_3-Flark_3	0.752	1.000	0.629
String_1-Flark_3	0.000	0.000	0.000
String_2-Flark_3	0.000	0.000	0.000
String_3-Flark_3	0.005	0.000	0.000
Lawn_2-Lawn_1	0.921	0.041	0.005
Lawn_3-Lawn_1	0.000	0.000	0.000
String_1-Lawn_1	0.607	0.004	0.000
String_2-Lawn_1	0.928	0.000	0.000
String_3-Lawn_1	0.996	1.000	0.999
Lawn_3-Lawn_2	0.000	0.000	0.000
String_1-Lawn_2	1.000	0.999	0.919
String_2-Lawn_2	1.000	0.000	0.000
String_3-Lawn_2	0.436	0.202	0.000
String_1-Lawn_3	0.000	0.000	0.000
String_2-Lawn_3	0.000	0.000	0.000
String_3-Lawn_3	0.000	0.000	0.000
String_2-String_1	0.999	0.000	0.000
String_3-String_1	0.138	0.036	0.000
String_3-String_2	0.441	0.000	0.000

Table 8. Tukey HD tables for ANOVA test results with vegetation type and plot as a grouping factor for redox potential. P values under the significance limit of 0.05 are marked with red.

Comparison	Redox 40 cm	Redox 25 cm	Redox 15 cm	Redox 5 cm
Flark-String	0.000	0.000	0.000	0.000
Lawn-String	0.000	0.000	0.000	0.000
Lawn-Flark	0.000	0.000	0.083	0.000
Flark_2-Flark_1	0.010	0.945	0.999	0.046
Flark_3-Flark_1	0.000	0.000	0.920	1.000
Lawn_1-Flark_1	0.000	0.000	0.000	0.000
Lawn_2-Flark_1	0.000	0.001	0.994	0.600
Lawn_3-Flark_1	0.000	0.000	1.000	0.047
String_1-Flark_1	0.000	0.000	0.000	0.000
String_2-Flark_1	0.000	0.000	0.000	0.053
String_3-Flark_1	0.924	0.000	0.001	0.000
Flark_3-Flark_2	0.000	0.000	0.562	0.104
Lawn_1-Flark_2	0.000	0.000	0.000	0.000
Lawn_2-Flark_2	0.000	0.073	1.000	0.000
Lawn_3-Flark_2	0.000	0.000	1.000	0.000
String_1-Flark_2	0.002	0.000	0.000	0.000
String_2-Flark_2	0.000	0.000	0.000	1.000
String_3-Flark_2	0.000	0.000	0.000	0.000
Lawn_1-Flark_3	0.001	0.000	0.000	0.000
Lawn_2-Flark_3	0.000	0.000	0.409	0.423
Lawn_3-Flark_3	0.000	0.000	0.722	0.021
String_1-Flark_3	0.000	0.000	0.000	0.000
String_2-Flark_3	0.000	0.000	0.000	0.115
String_3-Flark_3	0.000	0.000	0.091	0.000
Lawn_2-Lawn_1	0.000	0.000	0.000	0.016
Lawn_3-Lawn_1	0.000	0.000	0.000	0.277
String_1-Lawn_1	0.000	0.000	0.000	0.000
String_2-Lawn_1	0.000	0.000	0.173	0.000
String_3-Lawn_1	0.000	0.000	0.000	0.000
Lawn_3-Lawn_2	0.000	0.615	1.000	0.968
String_1-Lawn_2	0.000	0.000	0.000	0.000
String_2-Lawn_2	0.000	0.000	0.000	0.000
String_3-Lawn_2	0.000	0.000	0.000	0.000
String_1-Lawn_3	0.000	0.000	0.000	0.000
String_2-Lawn_3	0.989	0.000	0.000	0.000
String_3-Lawn_3	0.000	0.000	0.000	0.000
String_2-String_1	0.000	0.000	0.000	0.000
String_3-String_1	0.000	0.394	0.000	0.395
String_3-String_2	0.000	0.000	0.234	0.000

Table 9. Correlations between variables included in modelling. Cells highlighted with green are corrections of a variable with themselves and cells highlighted with red are correlations that are over the line of 0.7.

	CH4_flux	Reco	GPP1200	Chamber_temperature	Soil_temperature	Air_temperature	WTP	Redox_40cm	Redox_25cm	Redox_15cm	Redox_5cm	Shrubs_LAI	Forbs_LAI	Graminoids_LAI	Sphagnum	Dry_mosses	Wet_mosses	Litter	Vascular_plant_LAI	Moss_cover	Relative_humidity	PAR	Preciptitation
CH4_flux	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Reco	0.19	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GPP1200	0.08	0.66	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chamber_temperature	0.29	0.61	0.19	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Soil_temperature	0.39	0.47	0.29	0.67	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Air_temperature	0.28	0.62	0.20	0.88	0.76	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
WTP	0.24	-0.41	-0.37	0.07	0.10	0.00	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Redox_40cm	0.11	0.00	0.15	0.03	0.10	0.02	-0.21	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Redox_25cm	-0.13	0.31	0.53	-0.02	-0.06	-0.02	-0.33	0.29	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Redox_15cm	-0.17	0.23	0.20	0.00	0.09	0.04	-0.39	-0.01	0.16	1.00	-	-	-	-	-	-	-	-	-	-	-	-	-
Redox_5cm	-0.30	0.02	-0.09	-0.07	-0.08	-0.03	-0.36	-0.13	-0.07	0.38	1.00	-	-	-	-	-	-	-	-	-	-	-	-
Shrubs_LAI	-0.27	0.31	0.29	-0.04	-0.03	0.01	-0.63	-0.20	0.35	0.56	0.56	1.00	-	-	-	-	-	-	-	-	-	-	-
Forbs_LAI	0.02	0.42	0.55	0.02	0.08	0.05	-0.54	-0.01	0.43	0.23	0.11	0.68	1.00	-	-	-	-	-	-	-	-	-	-
Graminoids_LAI	0.04	0.15	0.25	0.09	0.08	0.07	0.09	0.34	0.20	-0.22	-0.29	-0.37	-0.24	1.00	-	-	-	-	-	-	-	-	-
Sphagnum	0.01	0.24	0.36	-0.03	0.00	-0.01	-0.61	0.30	0.16	0.07	0.12	0.28	0.26	-0.21	1.00	-	-	-	-	-	-	-	-
Dry_mosses	-0.17	0.12	0.11	-0.02	-0.01	-0.01	-0.16	-0.22	0.35	0.63	0.39	0.57	0.23	-0.39	-0.19	1.00	-	-	-	-	-	-	-
Wet_mosses	0.14	-0.15	-0.27	0.01	-0.02	0.00	0.50	-0.23	-0.06	-0.20	-0.08	-0.32	-0.27	0.05	-0.67	0.12	1.00	-	-	-	-	-	-
Litter	-0.21	0.39	0.56	0.00	-0.01	0.01	-0.37	0.31	0.53	0.18	-0.18	0.04	0.17	0.54	0.06	0.05	-0.22	1.00	-	-	-	-	-
Vascular_plant_LAI	-0.17	0.46	0.55	0.02	0.05	0.05	-0.65	0.00	0.53	0.41	0.33	0.86	0.81	0.07	0.23	0.35	-0.33	0.34	1.00	-	-	-	-
Moss_cover	0.11	0.19	0.21	-0.02	-0.03	-0.01	-0.32	0.08	0.26	0.07	0.19	0.20	0.13	-0.34	0.55	0.18	0.22	-0.14	0.05	1.00	-	-	-
Relative_humidity	-0.37	-0.31	-0.25	-0.51	-0.36	-0.48	-0.21	-0.11	-0.13	0.04	0.21	0.04	-0.13	-0.05	0.00	0.03	0.00	0.05	-0.04	0.00	1.00	-	-
PAR	0.21	0.31	0.14	0.49	0.17	0.36	0.12	0.03	0.07	0.02	-0.10	0.01	0.10	0.01	-0.01	0.03	0.00	-0.02	0.05	0.00	-0.76	1.00	-
Preciptitation	-0.16	-0.07	-0.03	-0.15	0.00	0.01	-0.03	0.01	-0.04	0.00	0.07	-0.01	-0.04	0.00	0.00	-0.03	0.00	0.02	-0.02	0.00	0.24	-0.28	1.00

Table 10. Edf and p-values for all five initial models. P-values marked with color as follows: read when P < 0.002, orange when 0.01 > P > 0.001 and green when 0.05 > P > 0.01.

	M1		M2		M3		M4		M5	
	edf	p	edf	p	edf	p	edf	p	edf	p
GPP_{1200}	1.909	0.000	1.945	0.000	1.828	0.000	1.945	0.000	1.936	0.000
Chamber T	1.636	0.000	1.761	0.000	1.461	0.000	1.761	0.000	1.565	0.000
Soil T	1.857	0.000	1.894	0.000	1.855	0.000	1.894	0.000	1.920	0.000
WTP	1.949	0.000	1.983	0.000	1.923	0.001	1.983	0.000	1.978	0.000
Relative humidity	1.114	0.000	1.143	0.000	1.111	0.000	1.143	0.000	1.189	0.000
Precipitation	0.755	0.047	0.736	0.054	0.776	0.038	0.736	0.054	0.777	0.038
Redox 40 cm	1.255	0.000	1.472	0.000	1.254	0.000	1.472	0.000	1.470	0.000
Redox 25 cm	0.000	0.354	1.712	0.000	1.532	0.078	1.712	0.000	0.711	0.122
Redox 15 cm	0.000	0.326	0.000	0.345	0.661	0.083	0.000	0.345	0.000	0.850
Redox 5 cm	0.679	0.077	0.978	0.000	0.738	0.051	0.978	0.000	0.938	0.002
Shrubs LAI	1.424	0.000	-	-	1.470	0.000	-	-	-	-
Forbs LAI	1.769	0.000	-	-	1.777	0.000	-	-	-	-
Graminoids LAI	0.000	0.333	-	-	1.646	0.150	-	-	-	-
Vascular plant LAI	-	-	1.873	0.000	-	-	1.873	0.000	-	-
Dry mosses	1.633	0.078	-	-	-	-	0.000	0.605	-	-
Sphagnum	0.000	0.252	-	-	-	-	0.000	0.916	-	-
Wet mosses	0.479	0.165	-	-	-	-	0.000	0.926	-	-
Moss cover	-	-	0.000	0.998	0.703	0.061	-	-	-	-
Litter	1.863	0.000	1.917	0.000	1.874	0.000	1.917	0.000	-	-
Vegetation type	-	-	-	-	-	-	-	-	0.000	0.594
Plot	6.327	0.000	7.604	0.000	6.789	0.000	7.604	0.000	7.626	0.000

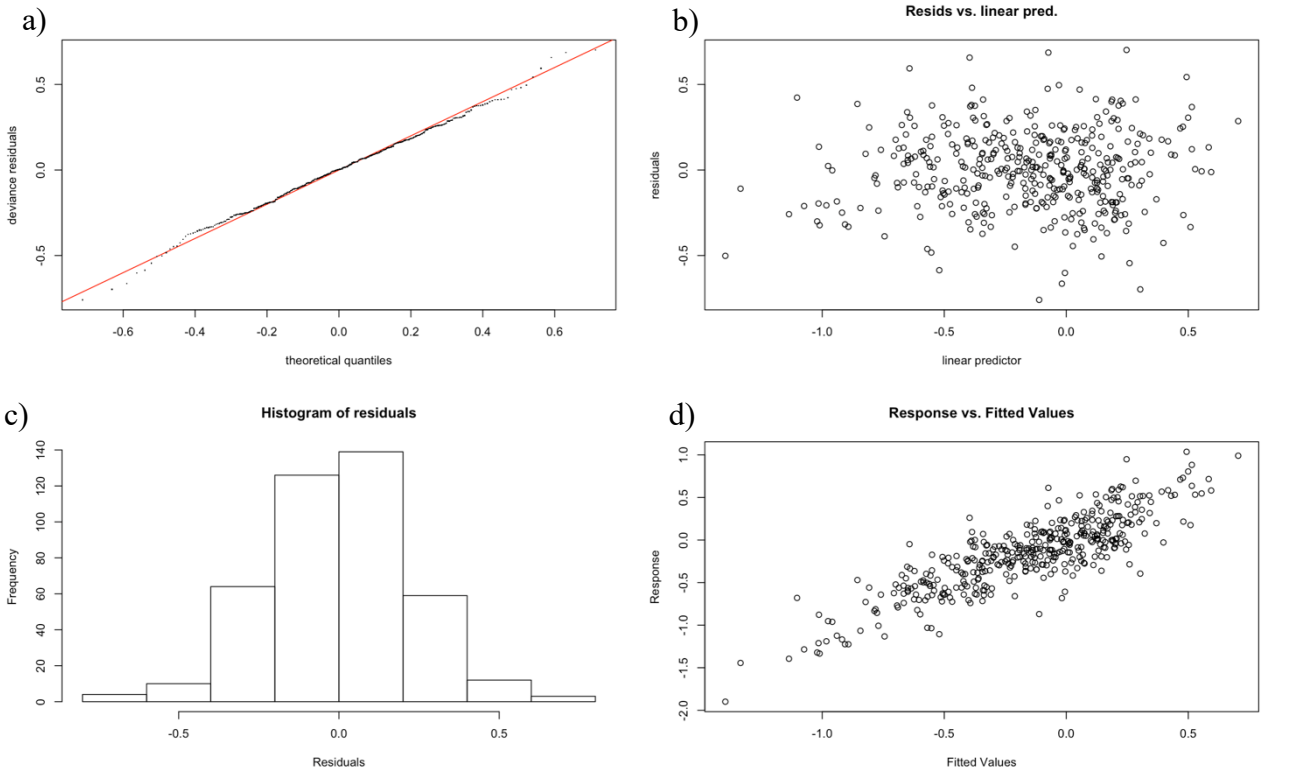

Figure 2. Plots form gam.check function in R. a) Q-Q plot, b) residuals of the model plotted again the linear predictor, c) histogram of residuals and d) response plotted against fitted CH_4 flux values.

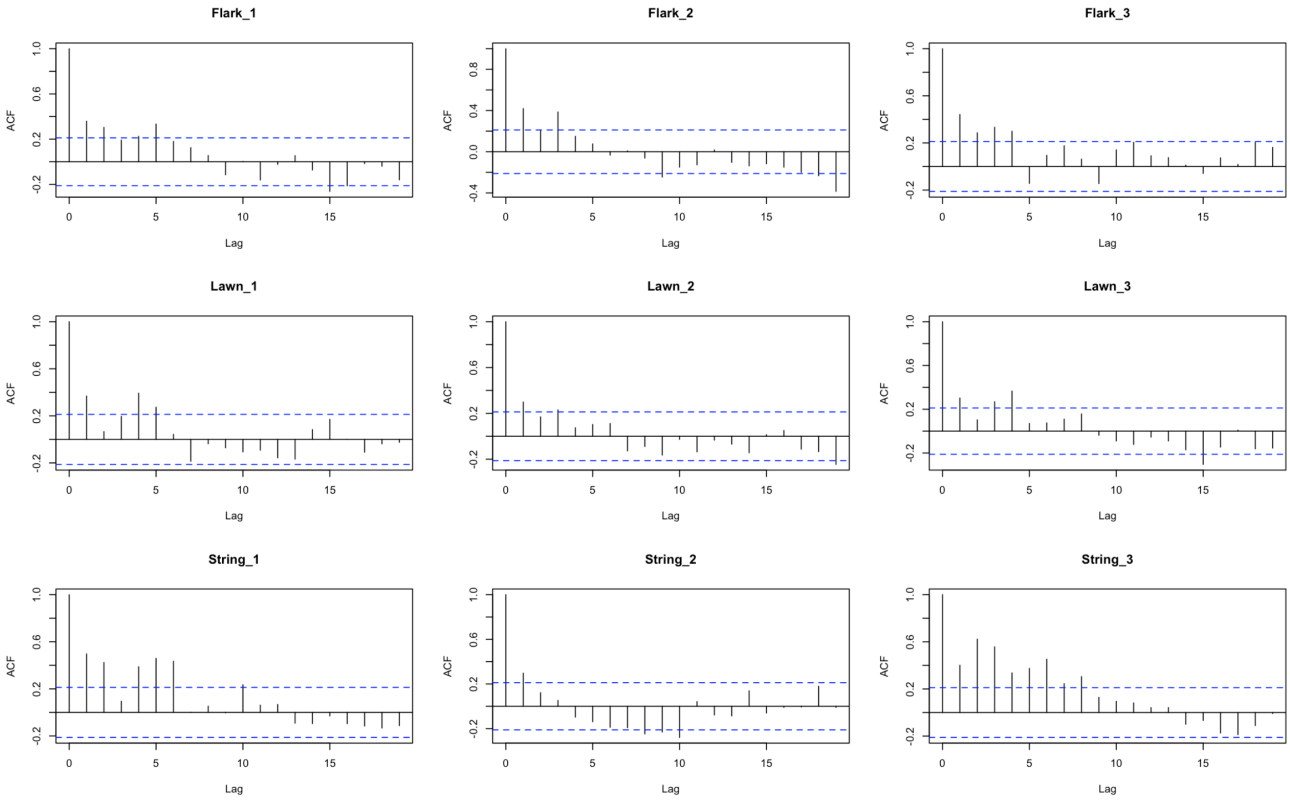

Figure 3. Temporal autocorrelation for residuals of Model 3 for each measurement plot. The lag (x-axis) represents days.